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THE UNIVERSITY OF ALBERTA

GASTRO-INTESTINAL HELMINTHS IN WHITE-TAILED DEER

(*ODOCOILEUS VIRGINIANUS*) AND MULE DEER

(*ODOCOILEUS HEMIONUS*) OF ALBERTA: A COMMUNITY APPROACH.

by



TERRANCE MICHAEL STOCK

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ABSTRACT

Gastro-intestinal helminths were collected from 60 white-tailed deer, *Odocoileus virginianus dacotensis*, and 60 mule deer, *Odocoileus hemionus hemionus*, from throughout Alberta. In addition, 13 Columbian black-tailed deer, *Odocoileus hemionus columbianus*, from Vancouver Island, British Columbia were examined for parasites. Mule deer had 16 species of helminths whereas whitetails were infected with 11 species, all of which were found in mule deer. Intensities of infection of all species of parasites were low. Black-tailed deer were infected with 11 species of parasites and possessed higher intensity infections than those found in deer of Alberta.

The helminth fauna of white-tailed deer was impoverished when compared with that reported from deer of other areas of North America. Infections in mule deer of Alberta were similar to those reported from the central part of the mule deer range. Explanations for species richness, diversity, and geographic distributional patterns based on relative host density and ecological interactions are provided.

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I. INTRODUCTION

Parasitological questions have been traditionally raised at the organism level of organization. Recently, an increasing number of investigations have been carried out on parasites at the population level (Tallis and Leyton, 1966, 1969; Nasell and Hirsh, 1972; Anderson, 1974, 1976a, 1976b). Many host surveys have been conducted and species lists compiled, but few attempts have been made to describe or determine the mechanisms involved in formation or regulation of parasite communities.

Among the reasons for this deficit is one of definition. Whereas individuals and populations are easily distinguished on morphological grounds, communities are more abstract constructs which suffer from having been assigned a variety of meanings (Ricklefs, 1973).

Two criteria should be met so that useful results can be obtained from studying communities: 1) the community should be an association of interacting populations (although structural similarity was shown between "real" vertebrate communities and communities generated from a neutral hypothesis model which excluded any interactions [Caswell, 1976]) and 2) the populations should be within clearly delimited boundaries (Ricklefs, 1973). In the present study, the helminth parasites inhabiting specified organs or organ systems of one species of host will be considered a community.

Another reason for the paucity of studies of parasite communities is the need for a more complete theoretical framework. As the theories of community structure of free-living organisms (Cody and Diamond, 1975)

are applied to parasitic systems, this framework will be developed. Presently however, Dogiel (1964) is one of the few workers who has attempted to generalize from the mass of information available. He hypothesized that:

"If a territory is inhabited by two host species whose characteristics (size, mode of life, type of feeding, etc.) allow them to harbour the same parasite fauna, but one of these hosts is a rare, sporadically occurring animal, while the other is one of the most common species in the locality, and if, in addition the ability of the parasites to infest and the susceptibility of the two hosts are the same, then the rarer animal will clearly have a smaller parasite fauna, producing infestations of lower intensity, since its parasites will have fewer chances of transmission from one host individual to another."

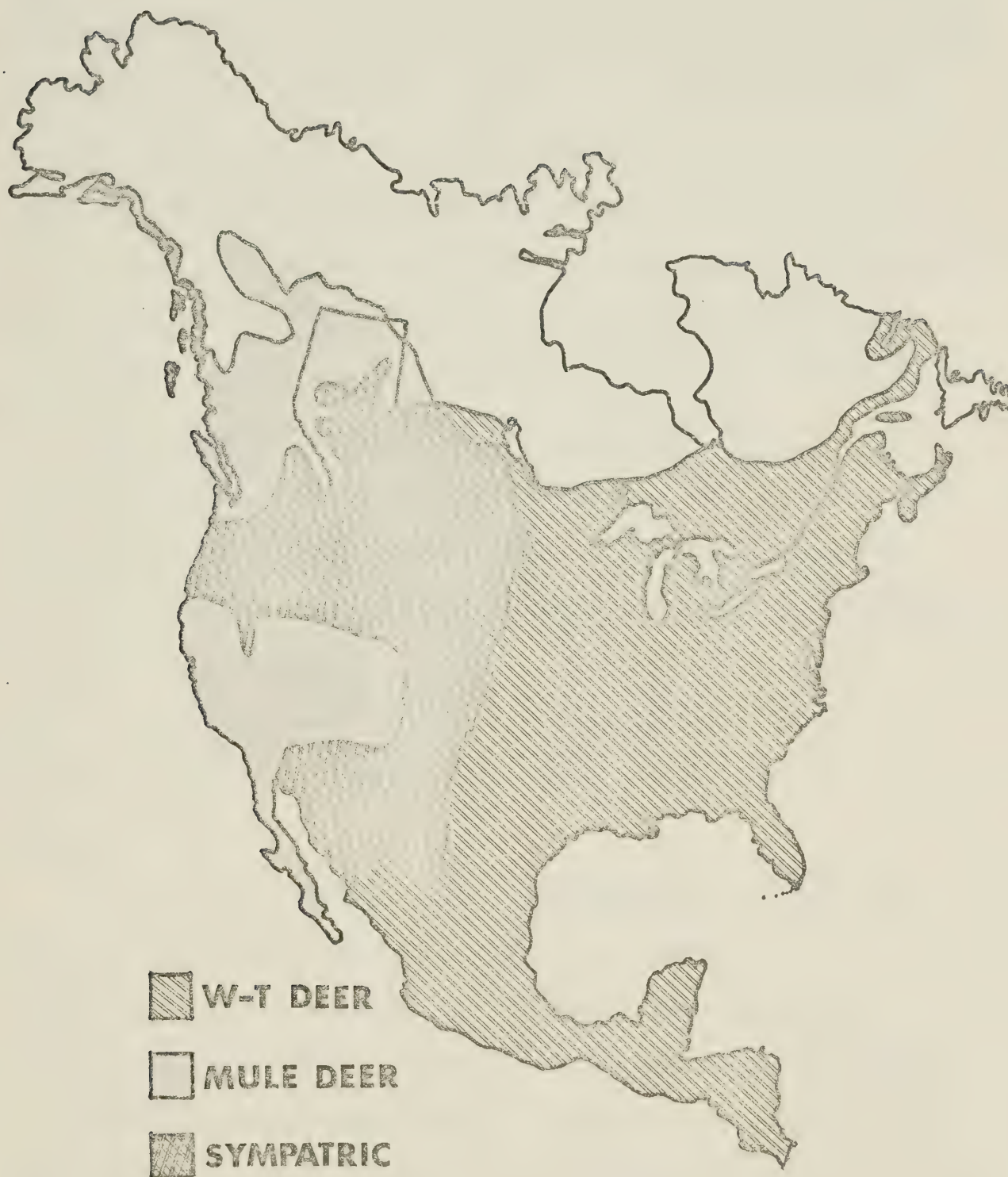
A corollary of Dogiel's hypothesis is, therefore, that host animals living near the extremes of their distributional range will have a poorer parasite fauna with lower intensity infections of fewer species.

Deer of the genus *Odocoileus* are ideal host candidates for testing Dogiel's hypothesis and its implications, particularly in Alberta. Both *Odocoileus hemionus* (Rafinesque) and *Odocoileus virginianus* (Zimmermann) are known to harbour many of the same parasites (Walker and Becklund, 1970) and both vary in population density throughout their ranges (Taylor, 1956). In Alberta, the two species are sympatric over much of the province and the northern edge of the white-tailed deer distribution lies within the present study area (Banfield, 1974) (Fig. 1).

Although these deer are economically significant big game species in Alberta, information on the composition, distribution and abundance of their gastro-intestinal parasites is rudimentary.

Cowan (1946, 1951) listed the helminths found during examination

Figure 1. Distribution of white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) in North America (from Banfield, 1974).



of 138 Columbian black-tailed deer, *Odocoileus hemionus columbianus*, from British Columbia and 8 mule deer, *O. hemionus*, and 2 white-tailed deer, *O. virginianus*, from "western Canada". Methods of examination, exact location of hosts, prevalence (proportion of animals infected) and intensity (mean number of worms per infected host) data were for the most part omitted in these papers. Stelfox (1962), in a non-technical paper on the parasites of big game animals in Alberta, mentioned the prevalence of some helminths "commonly" encountered in 21 "deer". Unfortunately, no further details on hosts or parasites were provided. Otherwise, there is little known about the gastro-intestinal parasites of either white-tailed or mule deer from Alberta.

Many surveys of deer parasites have been conducted in other parts of the range (see Walker and Becklund, 1970), however, often the investigators limited themselves to a single organ system or genus or species of parasite. Frequently, intensity and prevalence data have been incomplete. Nevertheless, the large number of surveys has ensured that enough information is available to compare the parasite communities from different parts of the host's distributional range.

In view of the pivotal position of Alberta in the geographic distribution of both white-tailed and mule deer of North America with respect to Dogiel's hypothesis, the lack of basic information on the helminth fauna of deer of the area and availability of information on deer parasites from other regions of North America, major goals of this study were, to: 1) identify and determine the abundance and distribution of the gastro-intestinal parasites of white-tailed and

mule deer in Alberta; 2) characterize the parasite communities as has been done for free-living organisms; and 3) compare and contrast the helminth faunas of deer from Alberta with those from other parts of the hosts' ranges and in so doing judge the validity of Dogiel's hypothesis.

II. MATERIALS AND METHODS

SOURCE OF SAMPLES

Viscera of 60 white-tailed and 60 mule deer were obtained in 1975, 1976 and 1977 through the co-operation of the Alberta Fish and Wildlife Division (Appendices I and II). Deer killed on highways throughout the province and deer killed by hunters in a military installation, Camp Wainwright, Alberta were collected (Fig. 2). Samples were frozen until necropsy. In addition, the frozen viscera of 13 Columbian black-tailed deer were obtained from two sites on Vancouver Island (Fig. 2) by the British Columbia Fish and Wildlife Branch in 1976 and 1977 (Appendix III).

Whenever possible, sex, date and location of capture, and age in months (estimated from cementum layers in sectioned incisors, Douglas (1968)), were recorded. Deer from Alberta were assigned to one of 5 natural biomes (Fig. 3). Distribution of these habitat zones was based on information synthesized from the maps of Soper (1964), Drinkwater (1969) and Hardy (1971).

NECROPSY TECHNIQUES

Standard necropsy techniques, as outlined by Samuel and Beaudoin (1966), Prestwood *et al.* (1971), Uhazy and Holmes (1971) and Pursglove *et al.* (1976), were followed. Heart, lungs, trachea and esophagus were separated from the visceral mass. The heart was serially sectioned (approximately 1 cm.) and examined for tapeworm cysticerci as was the pericardium. The external surfaces of the trachea and lungs were examined grossly for tapeworm cysticerci and lungworm lesions. The

Figure 2. Source location of 60 white-tailed deer (*Odocoileus virginianus*), 60 mule deer (*Odocoileus hemionus*) in Alberta and 13 Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in British Columbia examined for gastro-intestinal helminths, 1975-1977.

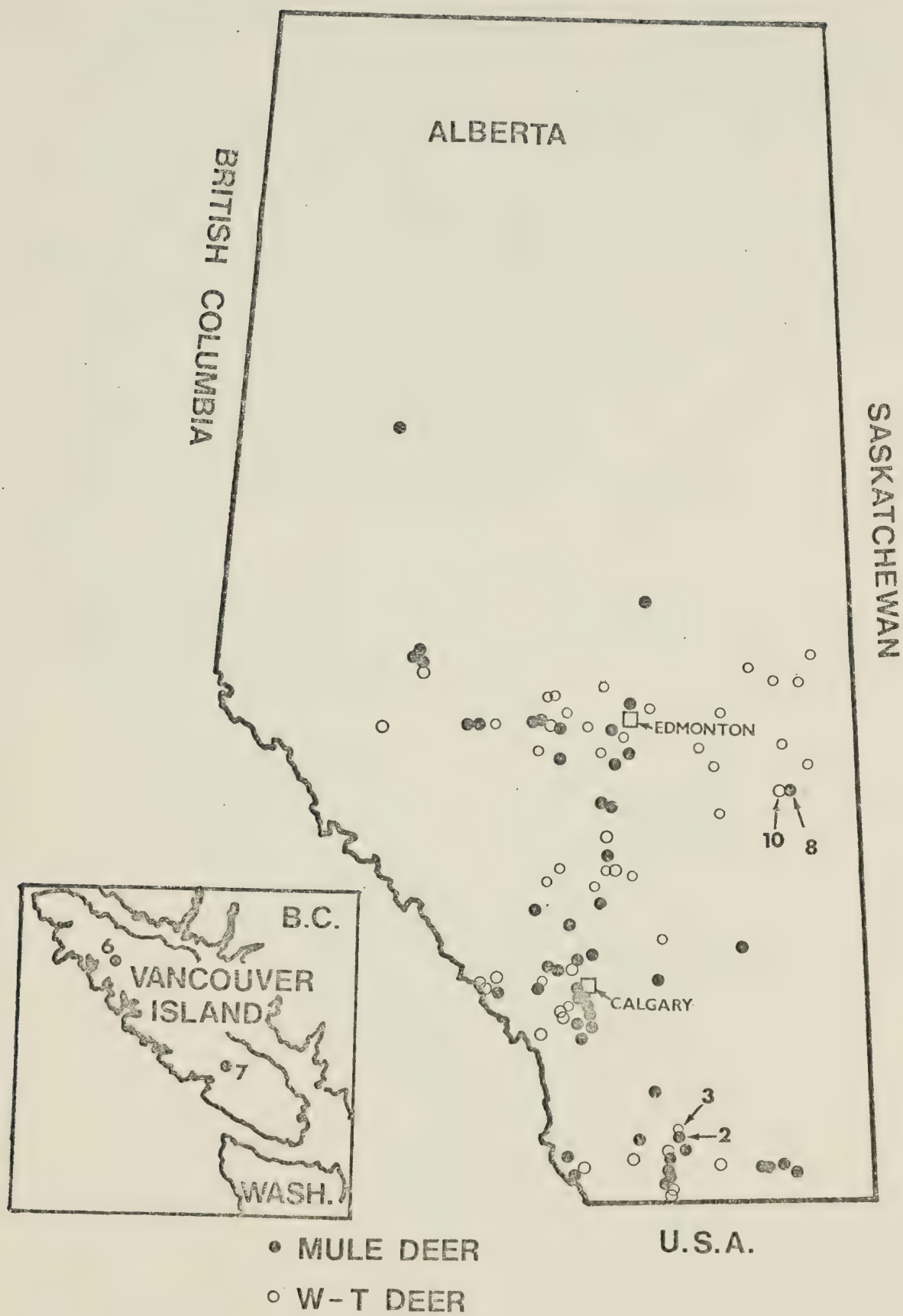
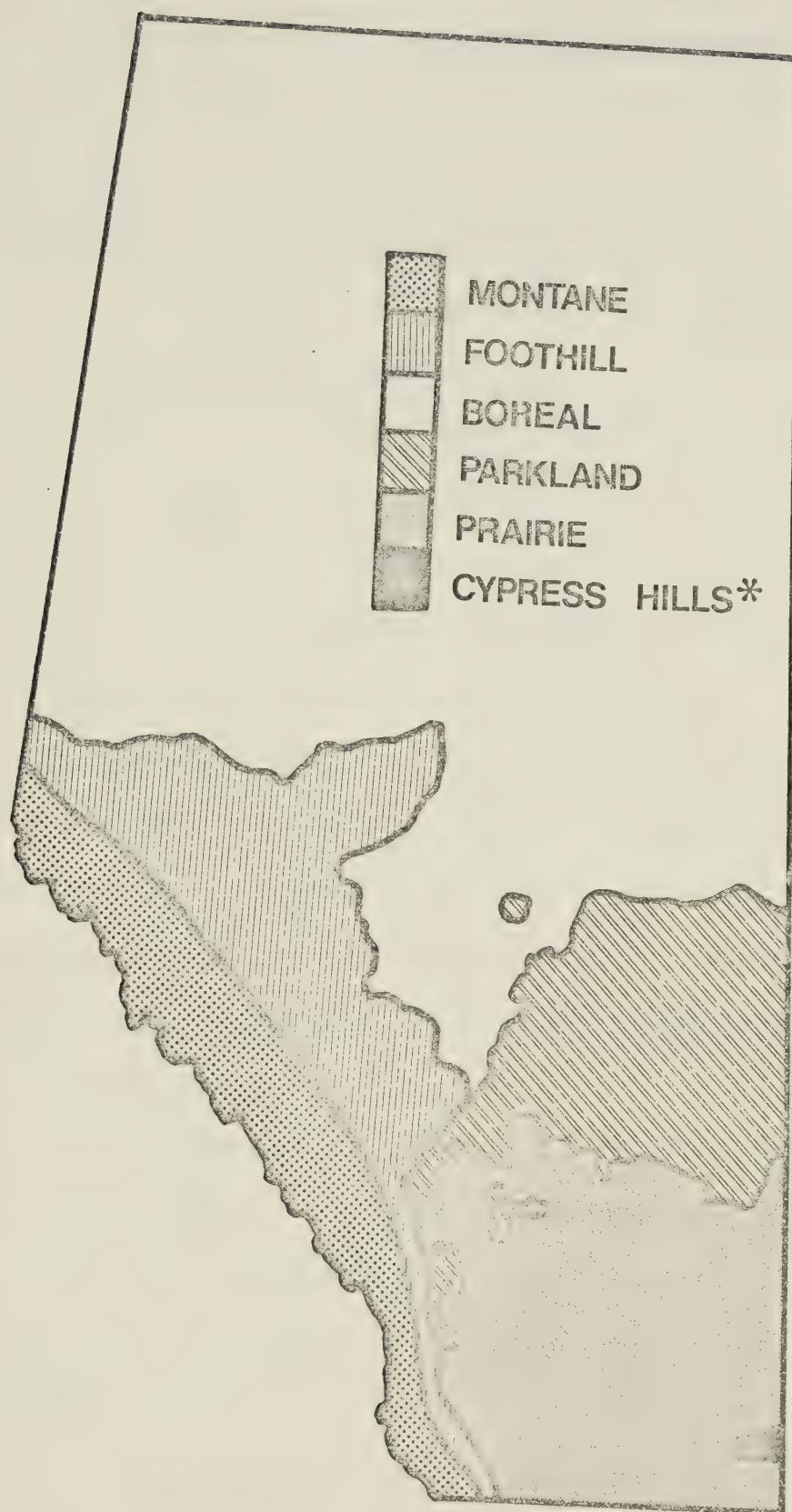


Figure 3. Habitat zones of Alberta.

(* No deer were examined from the Cypress Hills)



lungs were filled to excess with warm water and the contents emptied into a large container. The trachea, bronchi and larger bronchioles were cut, exposed and washed. Flushings from both sources were allowed to settle, decanted and examined for lungworms under 60X magnification of a dissecting microscope.

The esophagus was cut the entire length, opened, flushed to remove adhering food particles and examined for esophageal nematodes under 2X magnification and light.

The liver and common bile duct were removed from the remaining visceral mass. The bile duct was opened and examined for *Thysanosoma actinioides*. The external surface of the liver was examined for lesions caused by tapeworm cysticerci or liver fluke damage and then serially sectioned (approximately 1 cm.) for these parasites.

The mesenteries and all intestinal external surfaces were examined grossly for *Setaria* spp. and cysticerci. The greater omentum was cut from the left longitudinal groove of the rumen and from the descending duodenum and removed (Habel, 1975). It was then flushed with water to remove any contaminating rumen contents and examined under 2X magnification and light.

The small intestine was removed and separated into an anterior portion (approximately 1 m.) and the remaining posterior portion. Both portions were flushed and the linings examined for parasites under 2X magnification and light. The contents were passed through a graded series of sieves: 10 = 2.0 mm, 20 = 0.841 mm, 40 = 425 μ m and 80 = 180 μ m mesh (Canadian standard sieve series*). The strained

* W.S. Tyler Company, St. Catharines, Ont.

material and worms were flushed off the sieves into buckets and repeatedly washed and decanted until the supernatant was clear. The concentrate was then examined for parasites under the dissecting microscope (120X to 500X).

The caecum and large intestine were separated and flushed. The contents were repeatedly washed and decanted until the supernatant was clear. The concentrate was examined in the same manner as that from the small intestine. The large intestinal and caecal mucosae were examined under a lighted magnifier for nematodes.

The abomasum was removed from the other stomachs and opened along the greater curvature. Contents were flushed into a bucket and poured through sieves. The sieve contents were washed and decanted repeatedly until a concentrate was attained. The concentrate was examined at 120X to 150X under a dissecting microscope. The abomasal mucosa was divided into pyloric and fundic regions and scraped with a dull scalpel. The scrapings were examined under a dissecting microscope (120X to 500X).

The rumen was split along the greater curvature. Rumen contents were removed and the lining was examined grossly for rumen flukes.

Nematodes were counted, sexed and preserved in 70% ethyl-alcohol containing 5% glycerin for later examination. Cestodes were fixed in aceto-alcohol-formalin (AFA) and stained in Harris' haematoxylin, Semichon's acetocarmine, Blachin's stain or Grenacher's borax carmine. Nematodes were cleared in lacto-phenol beechwood creosote (1:1), cestodes in methyl salicylate. Identifications of nematodes and cestodes were made using the following keys and descriptions of parasite morphology: Ransom (1911); Ackert and Muldoon (1920);

May (1910); Dikmans (1931, 1935, 1936, 1941, 1957); Dougherty and Goble (1946); Olsen (1950); Olsen and Tolman (1950); Skrjabin et al. (1951, 1954, 1960); Sweatman and Plummer (1957); Swiatlikowski (1958, 1961); Becklund and Walker (1967a, 1967b, 1968, 1969, 1971); Wardle and McLeod (1968); Dronik (1971); Springfellow (1970, 1971); Verster (1969); Purglove et al. (1974); Lichtenfels (1977); and Anderson (1973).

When concurrent infections of morphologically similar nematodes were encountered, all worms present were counted and all males were separated by species and counted. An 1:1 sex ratio was assumed so that an estimate of the total number of individuals of each species present could be made.

DATA ANALYSIS

Data were analysed statistically on an IBM 360 computer using SPSS. Data related to host age, when available, were analysed for correlations with helminth fauna directly as well as grouped. Deer aged 1 to 11 months were considered fawns; 12 to 23 months, yearlings and 24 months and older, adults. Similarly, date of capture was analysed directly and grouped. Deer killed in September, October or November were grouped as an autumn sample; December, January or February as winter; March, April or May as spring and June, July or August as summer (Appendices I and II).

Number of worms and number of species of parasites were correlated with age, sex, season of capture and habitat zone using analysis of variance. A $\log_{10}(x + 1)$ transformation was applied to the data to reduce heteroscedasticity which was confirmed by

Bartlett's test (Snedecor and Cochran, 1967). Other methods of analysis of the data are given when first used.

III. RESULTS

GENERAL OVERVIEW OF HELMINTH FAUNA

Alberta

In total, 22 (37%) of the 60 white-tailed deer examined were infected with one or more helminth parasites. Eleven species, including 9 nematodes and 2 cestodes, were found (Table I). White-tails were generally lightly infected having a mean of 0.6 species per deer with a maximum of 3 per deer. *Trichostrongylus axei* was the most prevalent parasite (12%) in whitetails (Table I and Fig. 4). Since no males were found, specimens of the whipworm, genus *Trichuris*, remained the only helminth that could not be identified to species.

Mule deer were infected with 16 species of helminths including 13 nematodes and 3 cestodes. Fifty-two (87%) of the 60 mule deer examined were infected with a mean of 1.6 species per deer and a maximum of 6 per deer. The most prevalent parasite found was the abomasal worm, *Ostertagia ostertagi* (22%). Other prevalent parasites included *Taenia hydatigena* cysticerci (20%), the pinworm, *Skrjabinema parva* (17%) and *Ostertagia bisonis* (17%) (Table I and Fig. 4).

Although mule deer were host to all of the parasites found in white-tailed deer, there were differences in the abundance of the worms in the two host species. Differences are easily visualized by constructing parasite profiles (Levine, 1963). These plot the relative abundance (i.e., proportion of the total number of worms found) of each species in the same order. In white-tailed deer, the lungworm *Dictyocaulus viviparus* emerged as the most abundant member

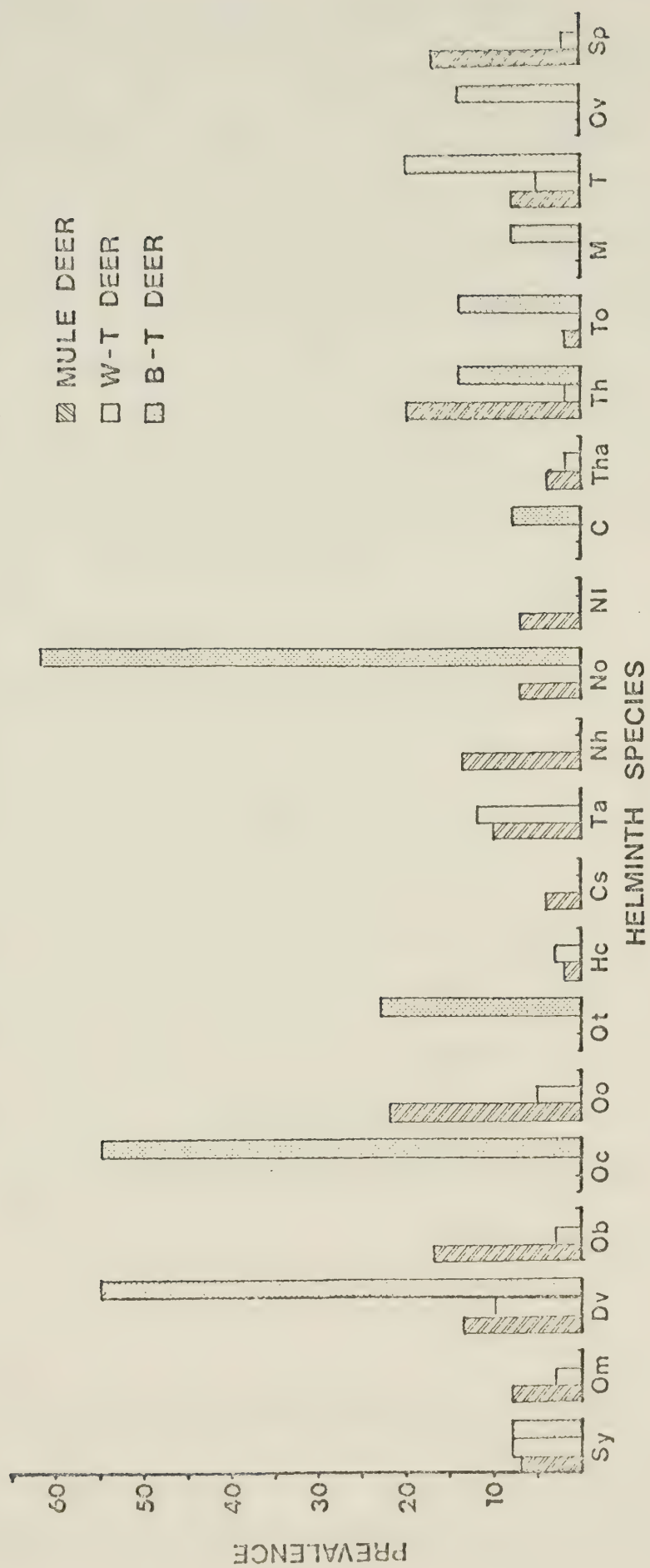
TABLE I. Prevalence and intensity of gastro-intestinal helminths in 60 white-tailed deer (*Odocoileus virginianus*), 60 mule deer (*Odocoileus hemionus*) from Alberta, 1975-77 and 13 black-tailed deer, (*Odocoileus hemionus columbianus*) from Vancouver Island, British Columbia, 1967-77.

	MULE DEER			WHITE-TAILED DEER			BLACK-TAILED DEER		
	% Infected	Intensity	Range*	% Infected	Intensity	Range	% Infected	Intensity	Range
NEMATODES									
<i>Setaria yehi</i>	7	1	(1-2)	8	2	(1-6)	8	8	(8)
<i>Orthostromylus macrostis</i>	8	6	(1-23)	3	9	(1-17)	0		
<i>Dictyocaulus viviparus</i>	13	4	(1-22)	10	10	(1-46)	54	35	(1-231)
<i>Ostertagia bisonis</i>	17	4	(1-9)	2**	2	(2)	0		
<i>Ostertagia circumcincta</i>	0			0			54	61	(2-272)
<i>Ostertagia ostertagi</i>	22	8	(1-40)	5	1	(1)	0		
<i>Ostertagia trifurcata</i>	0			0			23	11	(1-31)
<i>Haemonchus contortus</i>	2	2	(2)	3	6	(6)	0		
<i>Cooperia burnabadi</i>	3	2	(1-2)	0			0		
<i>Trichostrongylus axei</i>	10	5	(1-7)	12	3	(1-9)	0		
<i>Nematodirus helvetianus</i>	13	24	(1-123)	0			0		
<i>Nematodirus odocotlei</i>	7	158	(21-330)	0			62	114	(2-527)
<i>Nematodirus longissimespiculata</i>	7	176	(37-482)	0			0		
<i>Capillaria</i> sp.	0			0			8	2	(2)
<i>Oesophagostomum venulosum</i>	0			0			15	145	(1-289)
<i>Trichouris</i> sp.	8	1	(1-3)	5	1	(1-2)	23	4	(1-7)
<i>Skjabinema parva</i>	17	125	(1-1125)	2	1	(1)	0		
CESTODES									
<i>Moniezia</i> sp.	0			0			8	3	(3)
<i>Thysanosoma actinioides</i>	3	31	(2-60)	2	2	(2)	0		
<i>Taenia hydatigena</i>	20	1	(1-4)	2	2	(2)	15	1	(1)
<i>Taenia omissa</i>	2	1	(1)	0			15	8	(7-9)

* Range in number.

** New host record.

Figure 4. Prevalence (proportion of animals infected) of gastro-intestinal helminths in 60 white-tailed deer (*Odocoileus virginianus*), 13 black-tailed deer (*Odocoileus hemionus columbianus*), and 60 mule deer (*Odocoileus hemionus*). Sy = *Seteria yehi*, Om = *Orthostrongylus macrotis*, Dv = *Dictyocaulus viviparus*, Ob = *Ostertagia bisonis*, Oc = *Ostertagia circumcincta*, Oo = *Ostertagia ostertagi*, Ot = *Ostertagia trifurcata*, Hc = *Haemonchus contortus*, Cs = *Cooperia surnabada*, Ta = *Trichostrongylus axei*, Nh = *Nematodirus helvetianus*, No = *Nematodirus odocoilei*, Nl = *Nematodirella longissimespiculata*, C = *Capillaria* sp., Tha = *Thysanosoma actinioides*, Th = *Taenia hydatigena*, To = *Taenia omissa*, M = *Moniezia* sp., T = *Trichuris* sp., Ov = *Oesophagostomum venulosum*, and Sp = *Skrjabinema parva*.



of the helminth fauna (Fig. 5). *Trichostrongylus axei* and *Orthostrongylus macrotis* (= *Protostrongylus macrotis*) were also relatively abundant. *Skrjabinema parva* and all of the cestodes were minor components of the helminth community.

The helminth fauna of mule deer displayed a different pattern (Fig. 5). *Skrjabinema parva* was the most abundant parasite. The intestinal nematodes, *Nematodirus helvetianus*, *N. odocoilei* and *Nematodirella longissimespiculata*, which were absent in whitetails, accounted for 53% of the relative abundance in the mule deer helminth community.

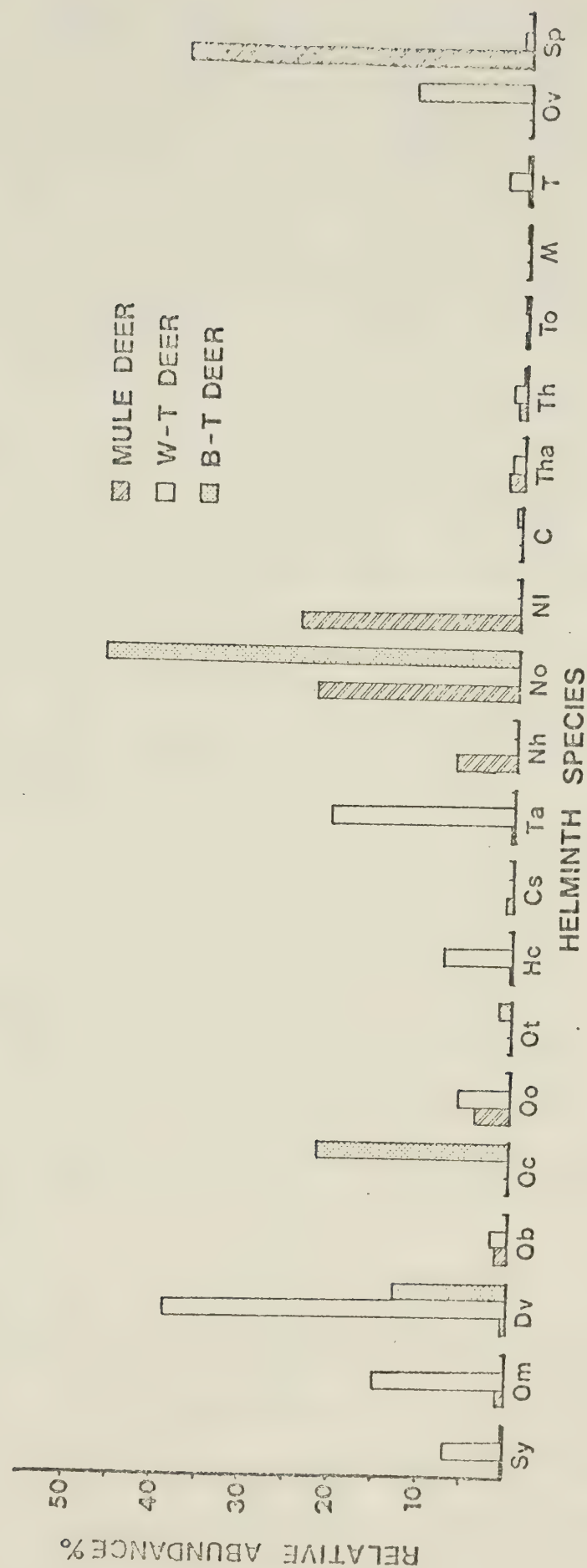
British Columbia

All of the 13 Columbian black-tailed deer examined were infected with one or more species of helminth. In total, 11 species were found including 8 nematodes and 3 cestodes (Table I). Black-tailed deer were infected with a mean of 2.9 species of helminth per deer and a maximum of 6 per deer. *Nematodirus odocoilei* was both the most prevalent and the most abundant parasite (Figs. 4, 5). It was not possible to identify *Capillaria* or *Trichuris* to species since no males were found. Specimens of the tapeworm *Moniezia* were poorly preserved and appeared to be immature; hence, specific identification was impossible.

PARASITE POPULATIONS

Communities by definition, are integrated ecological units composed of several populations of different species. To make any statements about communities as wholes, some consideration of the

Figure 5. Parasite profiles of gastro-intestinal helminths in 60 white-tailed deer (*Odocoileus virginianus*), 13 black-tailed deer (*Odocoileus hemionus columbianus*), and 60 mule deer (*Odocoileus hemionus*). Abbreviations as in the preceeding figure.



behavior of constituent parts should be attempted. In this section, the correlations between gastro-intestinal helminth populations and host sex and age, season of capture and habitat zone where captured will be considered.

In white-tailed deer, analysis of variance indicated that 62% of the variance in the number of parasite species, and 73% of the variance in the number of worms could be related to host sex and age, season of capture and habitat zone (Table II, III). These main effects alone, however, were responsible for only 15% and 19% of the variance in species and individuals, respectively, whereas interactions among the main effects accounted for 47% and 54%. The age-season interaction was the major factor accounting for variance in the number of parasites found ($F = 3.602$, $P = .017$). Of the main effects, season was the most highly related with the number of parasites.

In mule deer, main effects were more important than interactions in explaining the variance in both number of parasite species and the number of individual worms (Table IV, V). Sex was the most highly related factor ($F = 3.019$, $P = .095$), followed by habitat zone ($F = 1.753$, $P = .165$). Neither the season-sex interaction or the sex-habitat zone interaction accounted for much of the variance however (5% and 12% respectively).

Small sub-sample sizes made direct analysis or display of any relationships between the main effects and individual species or genera difficult. Raw data are presented in the form of "resource matrices" (Colwell and Futuyma, 1971) (Tables VI, VII), which attempt to characterize the spectrum and extent of use of resources by the

TABLE II. ANOVA table for the number of parasite species in white-tailed deer (*Odocoileus virginianus*), by habitat zone, age class, season of capture and sex of the host. Data were transformed by $\log_{10}(x+1)$. Higher order interactions were suppressed if empty cells or a singular matrix was encountered.

Source of Variation	Sum of Squares	DF	Mean Square	F	Prob. of F
MAIN EFFECTS	0.334	10	0.033	0.797	0.634
Habitat	0.207	4	0.052	1.235	0.328
Age	0.022	2	0.011	0.257	0.776
Season	0.092	3	0.031	0.728	0.547
Sex	0.014	1	0.014	0.323	0.576
2-WAY INTERACTIONS	1.044	25	0.042	0.996	0.510
Habitat Age	0.296	6	0.049	1.178	0.357
Habitat Season	0.319	7	0.046	1.085	0.409
Habitat Sex	0.218	4	0.055	1.300	0.304
Age Season	0.457	5	0.091	2.181	0.097
Age Sex	0.000	1	0.000	0.000	1.000
Season Sex	0.083	2	0.041	0.989	0.389
3-WAY INTERACTIONS	0.009	1	0.009	0.226	0.640
Habitat Sex Season	0.009	1	0.009	0.226	0.640
EXPLAINED	1.387	36	0.039	0.919	0.599
RESIDUAL	0.839	20	0.042		
TOTAL	2.226	56	0.040		

TABLE III. ANOVA table for the number of worms in white-tailed deer (*Odocoileus virginianus*) by habitat zone, age, season of capture and sex of hosts. Data were transformed by $\log_{10}(x+1)$. Higher order interactions were suppressed if empty cell or a singular matrix was encountered.

Source of Variation	Sum of Squares	DF	Mean Square	F	Prob. of F
MAIN EFFECTS	1.865	10	0.186	1.413	0.244
Habitat	0.554	4	0.138	1.049	0.407
Age	0.197	2	0.098	0.746	0.487
Season	0.822	3	0.274	2.078	0.135
Sex	0.048	1	0.048	0.365	0.552
2-WAY INTERACTIONS	5.260	25	0.210	1.595	0.145
Habitat Age	1.650	6	0.275	2.085	0.101
Habitat Season	1.232	7	0.176	1.334	0.286
Habitat Sex	0.806	4	0.202	1.527	0.232
Age Season	2.376	5	0.475	3.602	0.017
Age Sex	0.000	1	0.000	0.000	1.000
Season Sex	0.421	2	0.210	1.594	0.228
3-WAY INTERACTIONS	0.013	1	0.013	0.102	0.753
Habitat Age Season	0.013	1	0.013	0.102	0.753
EXPLAINED	7.138	36	0.198	1.503	0.168
RESIDUAL	2.639	20	0.132		
TOTAL	9.777	56	0.175		

TABLE IV. ANOVA table for the number of parasite species in mule deer (*Odocoileus hemionus*), by habitat zone, age class, sex, and season of capture of hosts. Data were transformed by $\log_{10}(x+1)$. Higher order interactions were suppressed if empty cells or a singular matrix was encountered.

Source of Variation	Sum of Squares	DF	Mean Square	F	Prob. of F
MAIN EFFECTS	0.517	10	0.052	1.549	0.171
Habitat	0.143	4	0.036	1.070	0.389
Age	0.149	2	0.074	2.228	0.125
Season	0.076	3	0.025	0.762	0.524
Sex	0.128	1	0.128	3.840	0.059
2-WAY INTERACTIONS	0.385	16	0.024	0.721	0.752
Habitat Age	0.084	5	0.017	0.506	0.769
Habitat Season	0.155	6	0.026	0.774	0.597
Habitat Sex	0.061	2	0.031	0.917	0.411
Age Sex	0.013	2	0.007	0.201	0.819
Season Sex	0.001	1	0.001	0.020	0.889
EXPLAINED	0.902	26	0.035	1.039	0.456
RESIDUAL	1.001	30	0.033		
TOTAL	1.903	56	0.034		

TABLE V. ANOVA table for the number of worms in mule deer (*Odocoileus hemionus*) by habitat zone, age class, season of capture, and sex of hosts. Data were transformed by $\log_{10}(x+1)$. Higher order interactions were suppressed if empty cells or a singular matrix was encountered.

Source of Variation	Sum of Squares	DF	Mean Square	F	Prob. of F
MAIN EFFECTS	8.322	10	0.832	1.583	0.160
Habitat	3.686	4	0.921	1.753	0.225
Age	1.649	2	0.824	1.568	0.225
Season	0.486	3	0.162	0.308	0.819
Sex	1.587	1	1.587	3.019	0.093
2-WAY INTERACTIONS	5.446	16	0.340	0.648	0.819
Habitat Age	2.364	5	0.473	0.900	0.494
Habitat Season	1.170	6	0.195	0.371	0.892
Habitat Sex	1.397	2	0.699	1.329	0.280
Age Sex	0.053	2	0.027	0.051	0.951
Season Sex	0.161	1	0.161	0.307	0.584
EXPLAINED	13.768	26	0.530	1.007	0.489
RESIDUAL	15.768	30	0.526		
TOTAL	29.536	56	0.527		

TABLE VI. Resource matrix of gastro-intestinal helminths of 60 white-tailed deer (*Odocoileus virginianus*) from Alberta.

Resource State	Species											
	Sy	Om	Dv	Ob	Oo	Hc	Ta	Tha	Th	T	Sp	TOTAL
HABITAT ZONE												
a) Parkland	2	0	3	0	4	0	28	0	2	4	0	43
b) Boreal	8	6	50	0	1	6	0	0	0	0	0	71
c) Prairie	0	17	7	1	4	6	1	2	0	0	0	38
d) Foothills	0	0	0	0	0	0	0	0	0	0	0	0
e) Montane	0	0	0	1	0	0	4	0	0	0	1	6
a) Male	8	0	51	0	5	0	8	2	0	2	0	76
b) Female	1	24	9	2	4	12	24	0	2	2	1	81
a) Fawn	1	6	2	0	5	12	5	0	2	3	0	36
b) Yearling	7	0	50	0	0	0	6	0	0	0	0	63
c) Adult	1	18	7	0	0	0	0	0	0	1	0	27
a) Summer	7	0	50	0	0	0	0	0	0	0	0	57
b) Autumn	2	17	9	0	1	0	1	0	2	3	0	35
c) Winter	1	0	1	2	8	0	31	2	0	1	1	47
d) Spring	0	7	0	0	0	12	0	0	0	0	0	19
a) Abomasum	0	0	0	2	9	8	30	0	0	0	0	49
b) Anterior Small Int.	0	0	0	0	0	0	2	2	0	0	0	4
c) Posterior Small Int.	0	0	0	0	0	1	0	0	0	0	0	1
d) Large Intestine	0	0	0	0	0	1	0	0	0	0	1	2
e) Caecum	0	0	0	0	0	0	0	0	0	4	0	4
f) Mesenteries	10	0	0	0	0	0	0	0	2	0	0	12
g) Liver	0	0	0	0	0	0	0	0	0	0	0	0
h) Lungs	0	24	60	0	0	0	0	0	0	0	0	84
TOTAL	48	119	299	8	41	58	140	8	10	20	4	755

TABLE VII. Resource matrix of gastro-intestinal helminths of 60 mule deer (*Odocoileus hemionus*) from Alberta.

Resource State		Species																
		Sy	Om	Dv	Ob	Oo	Hc	Ta	Cs	Nh	No	NL	Tha	Th	To	T	Sp	TOTAL
HABITAT ZONE	a) Parkland	3	3	3	11	31	2	3	2	8	0	121	2	4	0	0	1125	1318
	b) Boreal	2	23	1	0	12	0	2	1	11	0	482	0	3	1	0	0	538
	c) Prairie	0	0	23	22	52	0	2	0	163	21	0	60	5	0	6	1	355
	d) Foothills	0	5	2	3	0	0	0	0	10	0	0	0	4	0	0	0	24
	e) Montane	0	0	1	0	7	0	7	0	0	611	100	0	0	0	1	4	731
SEX	a) Male	1	3	28	24	94	2	11	2	138	571	231	62	9	1	6	1217	2400
	b) Female	3	28	6	12	9	0	4	1	54	61	482	0	7	0	1	8	676
AGE CLASS	a) Fawn	3	4	4	1	3	0	0	1	7	220	184	60	0	0	0	4	491
	b) Yearling	0	0	24	4	34	0	2	2	0	0	0	0	1	0	2	1125	1194
SEASON	c) Adult	0	1	3	1	40	2	1	0	10	0	0	0	0	0	1	5	64
	a) Summer	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
	b) Autumn	0	2	6	1	63	2	3	2	0	0	0	0	3	0	1	1131	1214
	c) Winter	3	24	23	34	26	0	5	0	181	82	603	62	12	1	5	91	1152
SITE	d) Spring	1	4	4	0	7	0	0	1	10	220	63	0	1	0	0	1	312
	a) Abomasum	0	0	0	35	94	2	15	0	0	1	0	0	0	0	0	0	147
	b) Anterior Small Int.	0	0	0	1	14	0	0	1	175	610	699	62	0	0	1	17	1580
	c) Posterior Small Int.	0	0	0	0	0	0	0	2	3	0	2	0	0	0	0	7	14
	d) Large Intestine	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	12
	e) Caecum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1190	1196
	f) Mesenteries	5	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	17
	g) Liver	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	5
TOTAL	h) Lungs	0	31	35	0	0	0	0	0	0	0	0	0	0	1	0	0	67
		21	129	164	149	486	10	55	15	770	2397	2967	308	66	14	30	5938	13509

parasites. Due to the nature of this study this attempt is crude, but it is hoped that the reader can refer to these matrices as well as the appendices for details of data distribution.

Number of *Nematodirus helvetianus* and *N. odocoilei* in mule deer varied significantly with season (Mann-Whitney $U = 20.5$, $P < 0.05$), showing a decrease from winter to spring. When habitat effects were controlled for, however, this trend lost significance (see below). The Mann-Whitney U test was used because it is a non-parametric statistic which assumes that samples come from populations having the same distribution (Sokal and Rohlf, 1969). *Ostertagia bisonis* and *O. ostertagi* also showed a seasonal trend in mule deer (Fig. 6), but this was not statistically significant. There appears to be one annual crop of *Ostertagia* spp., in which adults peak during the late summer and autumn. *Trichostrongylus axei* was more prevalent in winter (22%) than at any other season (3%) but, due to the low level infections found, variations in intensity could not be tested.

With one exception, sex did not appear to be importantly related with the intensity or prevalence of any helminths. *Nematodirella longissimespiculata* infections were more intense in female mule deer than in males (482 vs 74) but the single infected male precluded statistical analysis.

Age was not correlated with intensity or prevalence of any of the parasites. Similarly, age classes were not related. The low levels of parasite infection, coupled with the small sample size of accurately aged animals (69 out of 120) may have veiled any trends that were present.

Habitat zone was significantly related with intensity of *Nematodirus odocoilei* infections in mule deer. *N. odocoilei* were more numerous in deer from the montane zone than from deer of other habitat zones (204 vs 12) (Mann-Whitney U = 21, P = 0.02); even when seasonal influences were considered (Table VII). *Dictyocaulus viviparus* infections were more intense in mule deer from the prairies than elsewhere. A similar trend was not apparent for white-tailed deer. The whip worm, *Trichuris* sp. had a primarily southern distribution in Alberta. Infected whitetails were from the southern portion of the aspen parklands and 4 of the 5 infected mule deer were from the prairies.

Intensities of infection in the Camp Wainwright subsample did not differ significantly (P > .05) from that of deer from the remaining aspen parklands. Eighty-eight percent (7/8) of the mule deer from the Camp were infected as opposed to 85% (11/13) from the aspen parklands sample. Likewise, white-tailed deer from Camp Wainwright did not differ (P > .05) in prevalence of infection from those outside (5/10 vs 7/16) respectively.

Abundance patterns of the deer parasites differed to some extent. Mule deer in the Camp were infected with 9 species, all of which were of very low abundance except for *Skrjabinema parva* which dominated the helminth fauna (Fig. 7). Mule deer from the aspen parklands excluding Wainwright, harboured 11 species of which *N. longissimespiculata* and *S. parva* were dominant (Fig. 7). White-tailed deer from Camp Wainwright were infected with 4 species as opposed to 6 species from the parklands. One major difference in the abundance patterns was the absence of *T. axei* as well as other abomasal nematodes from the

Figure 6. Intensity of infection (± 1 S.E.) of *Ostertagia bisonis* and *Ostertagia ostertagi* in mule deer (*Odocoileus hemionus*) from the seasons of capture. A = Autumn, W = Winter, Sp = Spring, Su = Summer.

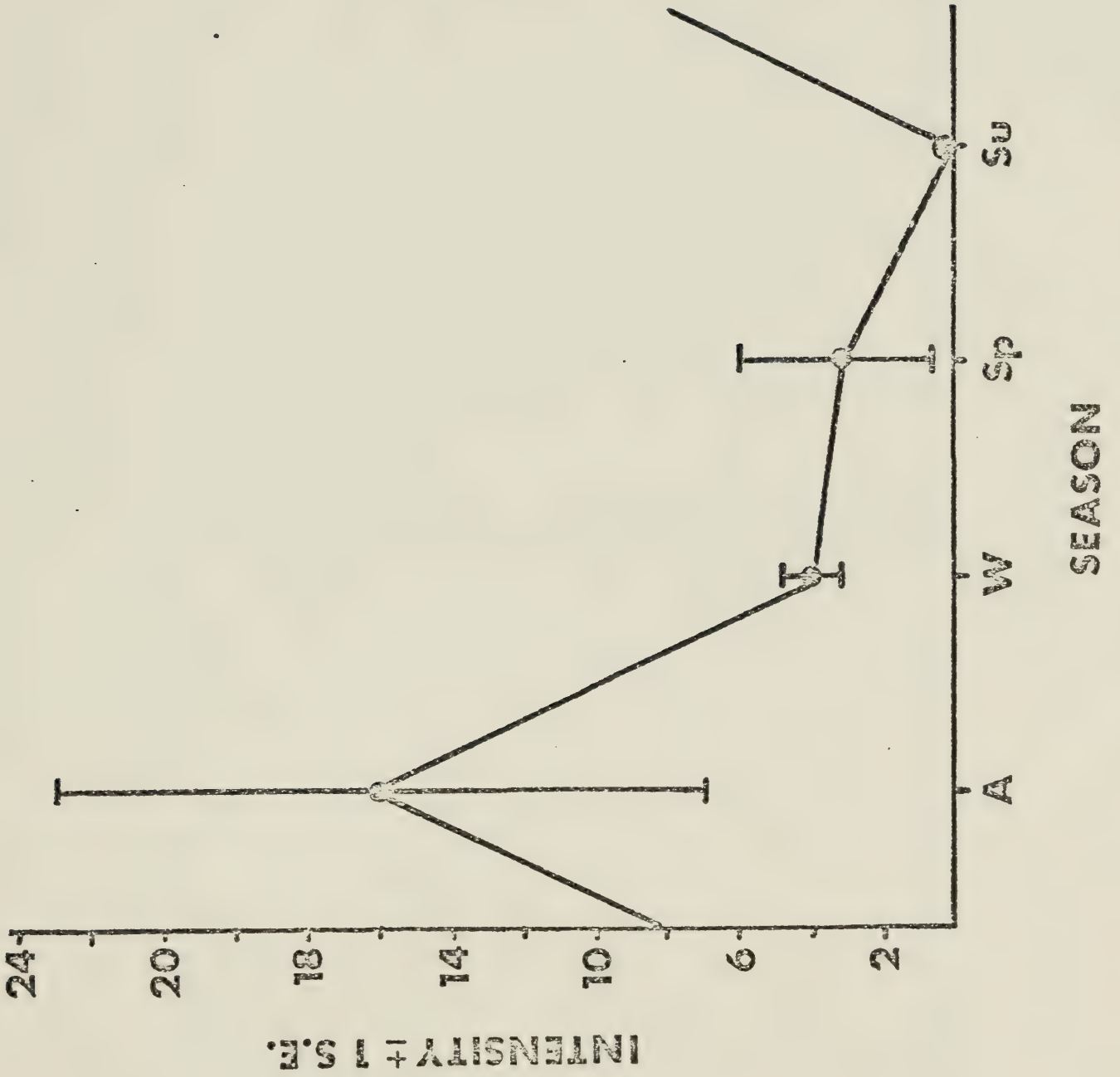
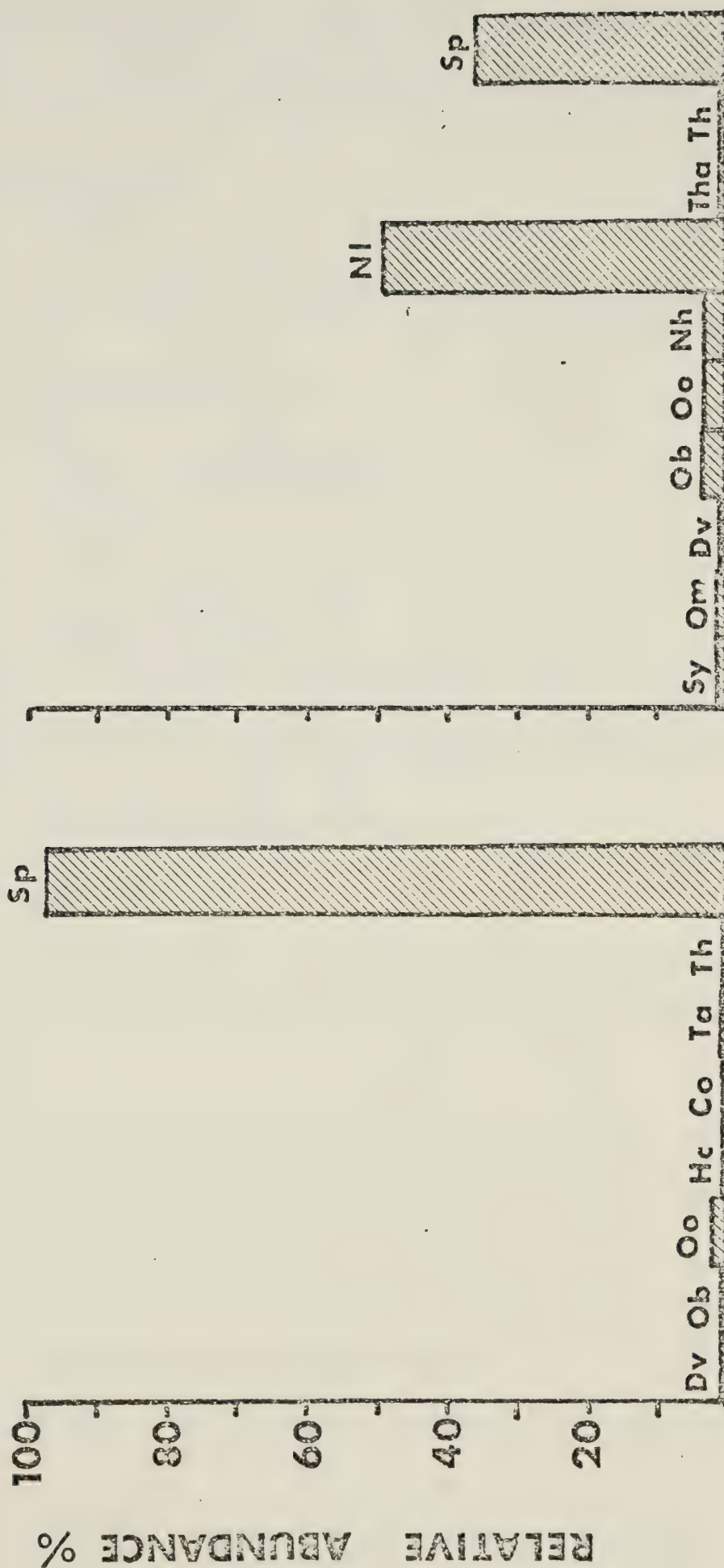


Figure 7. Parasite profiles of gastro-intestinal helminths from mule deer (*Odocoileus hemionus*) in Camp Wainwright, Alberta (N = 8) and in the aspen parklands excluding Wainwright (N = 13). Abbreviations as in Figure 4.

WAINWRIGHT

ASPEN PARKLAND



HELMINTH SPECIES

Camp (Fig. 8). *D. viviparus*, *T. hydatigena* and *Trichuris* sp. were all of equal abundance in Camp Wainwright.

COMMUNITY CHARACTERISTICS

Krebs (1972) identified 5 measurable characteristics of communities:

1. species diversity,
2. growth form and structure,
3. dominance,
4. relative abundance, and
5. trophic structure.

Although some of these attributes are not readily investigated in parasitic systems, there were several relevant characteristics that could be ascertained in this study.

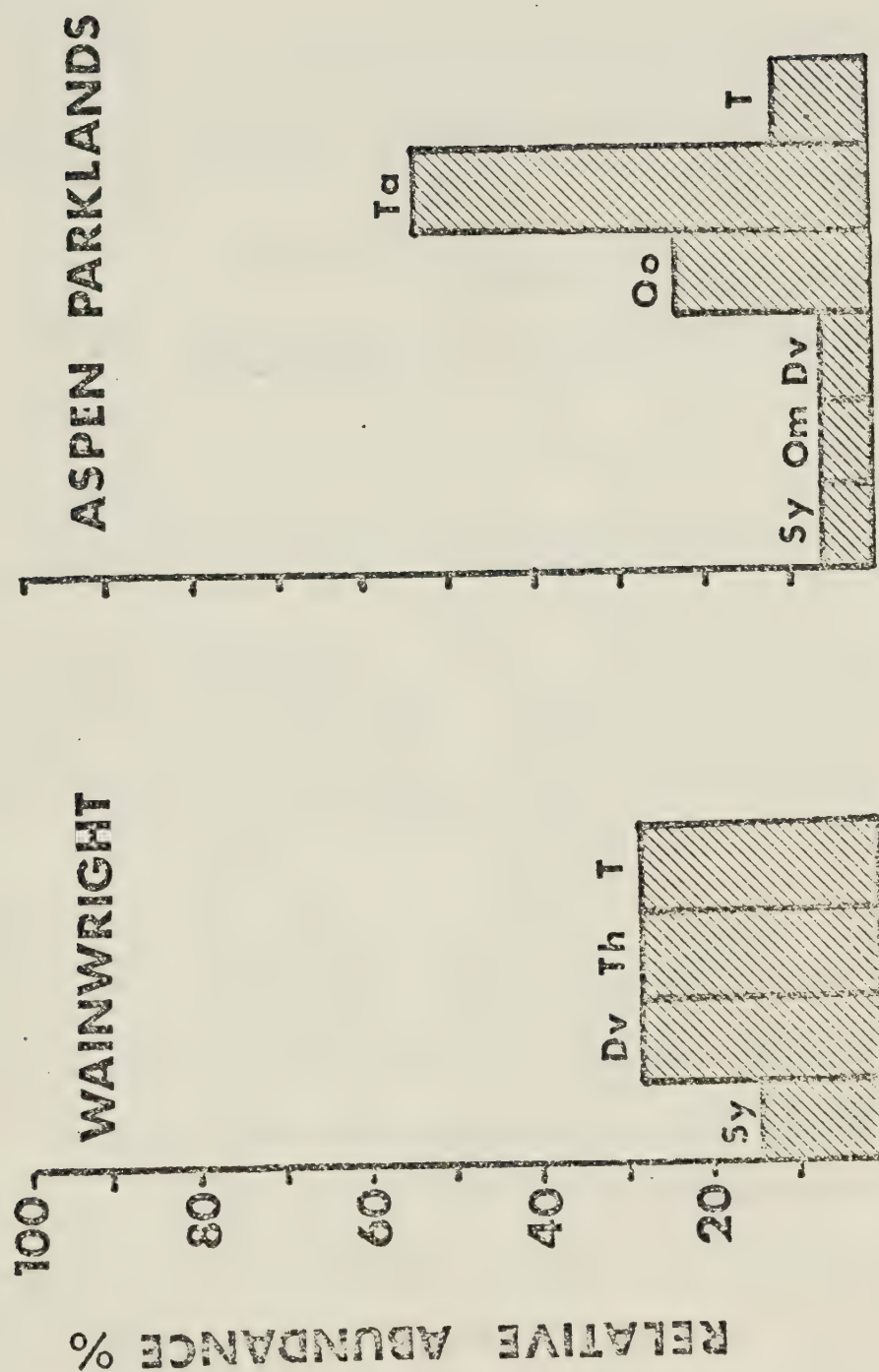
Species Diversity

Several measures of species diversity were computed including:

1. simple species richness (S), the number of species in the community,
2. areal species richness (R) (Whittaker, 1965), which as used by plant ecologists, was defined as average number of species present per unit area. Here, R is defined as the average number of species per deer (including uninfected samples). Since it is an average, R is amenable to statistical analysis,
3. Simpson's (1949) index of diversity (D), calculated as

$$D = 1 / \sum (Y_i / N)^2 \quad \text{where } Y_i \text{ is an importance value for species } i,$$

Figure 8. Parasite profiles of gastro-intestinal helminths from white-tailed deer (*Odocoileus virginianus*) in Camp Wainwright, Alberta (N = 10) and in the aspen parklands excluding Wainwright (N = 16). Abbreviations as in Figure 4.



HELMINTH SPECIES

in this case percent prevalence, and N is the total of the importance values for S species (as diversity increases, the magnitude of both H' and D increases),

4. Shannon-Weaver (1949) index of diversity (H'),
calculated as

$H' = - \sum P_i \ln P_i$ where P_i is the proportion of the community of S species represented by species i and $\ln$ is the natural logarithm, and

5. equitability (J), (Pielou, 1969), calculated as

$J = H'/H'_{\max}$ where H' is the Shannon-Weaver index and

$H'_{\max} = \ln S$.

All measures of species diversity were calculated for white-tailed, mule and black-tailed deer and are presented in Table VIII.

Growth Form and Structure

As defined by Krebs, this community characteristic is not readily interpretable in parasitic systems.

Dominance

Krebs (1972) characterized dominant species as, "... those which are highly successful ecologically and which determine to a considerable extent the conditions under which the associated species must grow." Therefore, a species may be functionally dominant in a community without being the most abundant species. No studies of functional dominance in parasitic systems have been made.

Several parasitologists including Gallimore (1964), Dogiel *et al.* (1964), Kisiielewski (1970) and Bush (1973) have attempted to define

TABLE VIII. Measures of diversity, equitability and species richness of gastro-intestinal helminths from mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*) from Alberta, and black-tailed deer (*Odocoileus hemionus columbianus*) from Vancouver Island, British Columbia.

	MULE	WHITE-TAILED	BLACK-TAILED
Species Richness (S)	16	11	11
Shannon-Weaver (H')	1.68	1.80	1.37
Shannon-Weaver (H' prev)	2.57	2.17	2.13
Equitability (J)	.60	.75	.57
Equitability (J prev)	.93	.91	.88
Simpson's Index (D)=(1-C)	.91	.87	.86
Areal Species Richness	1.58	.55	2.92

numerically dominant components of helminth communities. Bush (1973) was the first to propose a quantitative measure dominance, D_i .

$$D_i = \frac{Z_i}{\sum Z_i} \times 100$$

where Z_i (Janion, 1968) is an abundance index for species i in a community of S species.

$$Z_i = \frac{a \times b}{c^2}$$

where a is the total number of individuals of species i , b is the number of host individuals infected with species i and c is the total number of hosts examined.

Bush (1973) defined a dominant species as one which is characteristic of the community and has a D_i value greater than 1. Species for which D_i is between 0.01 to 0.99 were classified as co-dominants. Co-dominants make a significant contribution to the community, but can do well in other habitats (i.e., hosts). Another category, successful immigrants, include those species which occur infrequently, are not characteristic of the community, probably belong to another habitat, but develop and reproduce in the host under examination. They have D_i values between 0 and 0.009. Unsuccessful immigrants do not mature, contribute little to the community and are always characteristic of another habitat. D_i equals 0.

D_i values, Z_i values and dominance classification for white-tailed, black-tailed and mule deer gastro-intestinal helminths are listed in Tables IX, X, and XI. Based on Bush's (1973) criteria, ten species, *Setaria yehi*, *Orthostrongylus macrotis*, *Dictyocaulus viviparus*, *Haemonchus contortus*, *Trichostrongylus axei*, *Trichuris* sp., *Thysanosoma actinioides*, *Taenia hydatigena*, *Ostertagia bisonis* and *Ostertagia ostertagi* were dominant in whitetails. Although deer serve

TABLE IX. Abundance (Z_i) and dominance (D_i) measures of the gastrointestinal helminths from 60 white-tailed deer (*Odocoileus virginianus*) from Alberta. (Z_i and D_i calculated as in Bush, 1973.)

	Z_i	D_i	CLASSIFICATION
<i>Setaria yehi</i>	.0041	8.102	Dominant
<i>Orthostrongylus macrotis</i>	.0075	14.822	Dominant
<i>Dictyocaulus viviparus</i>	.0183	36.166	Dominant
<i>Ostertagia bisonis</i>	.0008	1.581	Dominant
<i>Ostertagia ostertagi</i>	.0016	3.162	Dominant
<i>Haemonchus contortus</i>	.0038	7.500	Dominant
<i>Trichostrongylus axei</i>	.0105	20.750	Dominant
<i>Trichuris</i> sp.	.0019	3.750	Dominant
<i>Skrjabinema parva</i>	.0005	0.988	Co-dominant
<i>Thysanosoma actinioides</i>	.0008	1.581	Dominant
<i>Taenia hydatigena</i>	.0008	1.581	Dominant

TABLE X. Abundance (Z_i) and dominance (D_i) measures of the gastrointestinal helminths of 60 mule deer (*Odocoileus hemionus*) from Alberta. (Z_i and D_i calculated as in Bush, 1973.)

	Z_i	D_i	CLASSIFICATION
<i>Setaria yehi</i>	.0025	.285	Co-dominant
<i>Orthostrongylus macrotis</i>	.0100	1.139	Dominant
<i>Dictyocaulus viviparus</i>	.0125	1.423	Dominant
<i>Ostertagia bisonis</i>	.0127	1.446	Dominant
<i>Ostertagia ostertagi</i>	.0322	3.667	Dominant
<i>Haemonchus contortus</i>	.0008	.091	Co-dominant
<i>Cooperia surnabada</i>	.0013	.148	Co-dominant
<i>Trichostrongylus axei</i>	.0058	.660	Co-dominant
<i>Nematodirus helvetianus</i>	.0555	6.320	Dominant
<i>Nematodirus odocoilei</i>	.1766	20.112	Dominant
<i>Nematodirella longissimespiculata</i>	.1963	22.355	Dominant
<i>Trichuris</i> sp.	.0033	.375	Co-dominant
<i>Skrjabinema parva</i>	.3427	39.027	Dominant
<i>Thysanosoma actinioides</i>	.0177	2.016	Co-dominant
<i>Taenia hydatigena</i>	.0077	.877	Co-dominant
<i>Taenia omissa</i>	.0005	.056	Co-dominant

TABLE XI. Abundance (Z_i) and dominance (D_i) measures of gastro-intestinal helminths from 13 black-tailed deer (*Odocoileus hemionus columbianus*) from Vancouver Island, British Columbia. (Z_i and D_i calculated as in Bush, 1973.)

	Z_i	D_i	CLASSIFICATION
<i>Setaria yehi</i>	.047	.062	Co-dominant
<i>Dictyocaulus viviparus</i>	10.024	13.294	Dominant
<i>Ostertagia circumcincta</i>	17.686	23.455	Dominant
<i>Ostertagia trifurcata</i>	.586	.777	Co-dominant
<i>Nematodirus odocoilei</i>	43.172	57.255	Dominant
<i>Capillaria</i> sp.	.012	.016	Immigrant
<i>Oesophogostomum venulosum</i>	3.432	4.552	Dominant
<i>Trichuris</i> sp.	.213	.282	Co-dominant
<i>Moniezia</i> sp.	.081	0.00	Unsuccessful*
<i>Taenia hydatigena</i>	.024	0.0003	Immigrant
<i>Taenia omissa</i>	.189	0.002	Immigrant

* Does not mature in this host.

only as intermediate hosts for *Taenia hydatigena*, the worms were considered as being mature in these hosts and, therefore, were treated in the same manner as adult stages of other parasites.

Skrjabinema parva was a co-dominant. In mule deer, 9 species were dominant including *Ostertagia bisonis* and *O. ostertagi*, *D. viviparus*, *Nematodirus helvetianus* and *N. odocoilei*, *Nematodirella longissimespiculata*, *S. parva*, *T. actinioides* and *O. macrotis*. Four species in blacktails were dominant; *D. viviparus*, *Ostertagia circumcincta*, *N. odocoilei* and *Oesophagostomum venulosum*.

To characterize abundance of a parasite species, one must consider both intensity and extensity of occurrence. Parasite profiles are probably the easiest way to visualize abundance of particular helminths within the framework of the entire parasite assemblage. Parasite profiles are plotted for white-tailed, black-tailed and mule deer (Fig. 5). In addition, profiles for deer from the different biomes of Alberta are presented in Fig. 9.

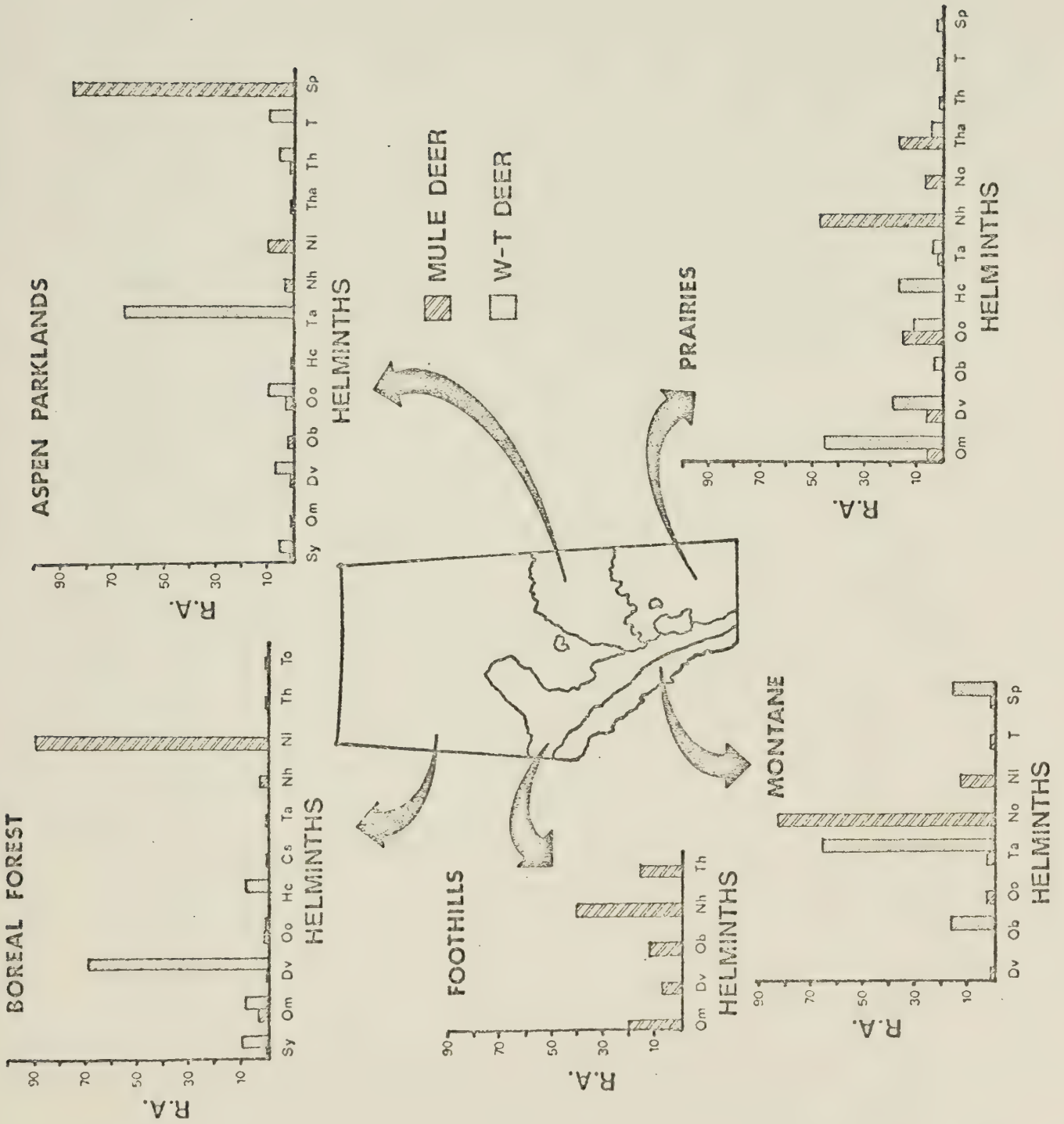
Trophic Structure

Parasite communities are unique in that there is no predation exerted on populations within a host. No energetics study was attempted, hence no comments can be made on trophic dynamics.

Taxonomy of helminths, however, is often based on the morphology of feeding structures. Therefore, the taxonomic make-up of a community of parasites does, to some extent, reflect the trophic structure.

As in all ruminants so far examined, the helminth communities of deer can be characterized as being composed primarily of direct

Figure 9. Parasite profiles of gastro-intestinal helminths of white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) from the biomes of Alberta. Abbreviations as in Figure 4.



life cycle, trichostrongylid nematodes. In whitetails, blacktails and mule deer respectively, 64, 69 and 64% of the species found were direct life cycle nematodes. Of these, 57, 73 and 46% belonged to the family Trichostrongylidae.

IV. DISCUSSION

The few significant correlations between parasite loads and host sex, host age and season of capture are not surprising. To thoroughly investigate the importance of any one of these factors a survey must be designed which restricts possible influences by the other factors. This natural experiment should then be supported by evidence from controlled experimental infections. Such was not the purpose of this study. Nevertheless, despite examination of adult nematodes only, small sample sizes and recovery of some parasites which, as a characteristic of their life style exhibit low intensity infection, several trends were indicated.

Samuel (1969) found that the average number of *Ostertagia odocoilei* and *O. mossi* increased in the fall and winter in white-tailed deer from southern Texas. The situation was reversed for mule deer of Alberta; that is, *Ostertagia* infections increased in the late summer. There are three possible explanations for this difference. Perhaps the seasonal dynamics of *Ostertagia* infections are correlated with an intrinsic property of the host species. This explanation seems unlikely since *O. ostertagi* infections in mule deer display the same seasonal pattern as infections in domestic cattle and sheep (Smith, 1974).

Conversely, the acquisition of adult parasites may correspond closely to climatic conditions. Temperatures in Texas in winter during Samuel's study were approximately 18° C. In Alberta, during summer months, the mean temperature was 15° C (figure based on data from Edmonton International Airport - standard monthly temperatures 1941-1974).

The optimum temperature for transmission of members of the genus *Ostertagia* varies from 5 to 22° C (Levine, 1963). In addition, when moisture requirements are considered, only December, January and February satisfy the conditions of maximum transmission for *Ostertagia* species in Texas (Fig. 10) while June, July and August are optimal months in Alberta (Fig. 11).

The third and most likely explanation for the seasonal trend in *Ostertagia* infections is one which combines both biotic and abiotic factors. Arrested development of L₄'s has been noted in *O. ostertagi* in cattle from eastern Canada (Smith, 1974) and *O. odocoilei*, *O. mossi* and *O. dikmansii* in deer from Ontario (Baker and Anderson, 1975). The "normal" seasonal variation of *Ostertagia* populations in northern regions, therefore, includes a marked decrease in the number of adult worms during the winter as was found in Alberta (or during excessively dry periods in hot, temperate areas).

The factors which induce arrested development are many and complex and may depend upon such factors as host immunological state, shifting food preferences, strain of parasite species, etc. (Schad, 1977). Thus, although simple bioclimatographic analysis is suggestive in this case, a complex of potentially interacting factors is possible.

Nematodirus odocoilei and *N. helvetianus* demonstrated an increase in the mean number of adults from winter to spring. This trend was not statistically significant when habitat zone of capture was considered. However, there is arrested development of *Nematodirus* spp. in sheep from Canada with the number of adult worms decreasing in winter (Ayalew and Gibbs, 1973). Thus the seasonal trend shown by *Nematodirus* spp. in deer, may be real.

Figure 10. Bioclimatograph of Welder Wildlife Refuge, Texas
(Meterological data from Samuel (1969)). Dotted line
delimits the region of maximum transmission of
Ostertagia species (Levine, 1963). Ordinate is mean
monthly temperature, abscissa is mean monthly
precipitation.

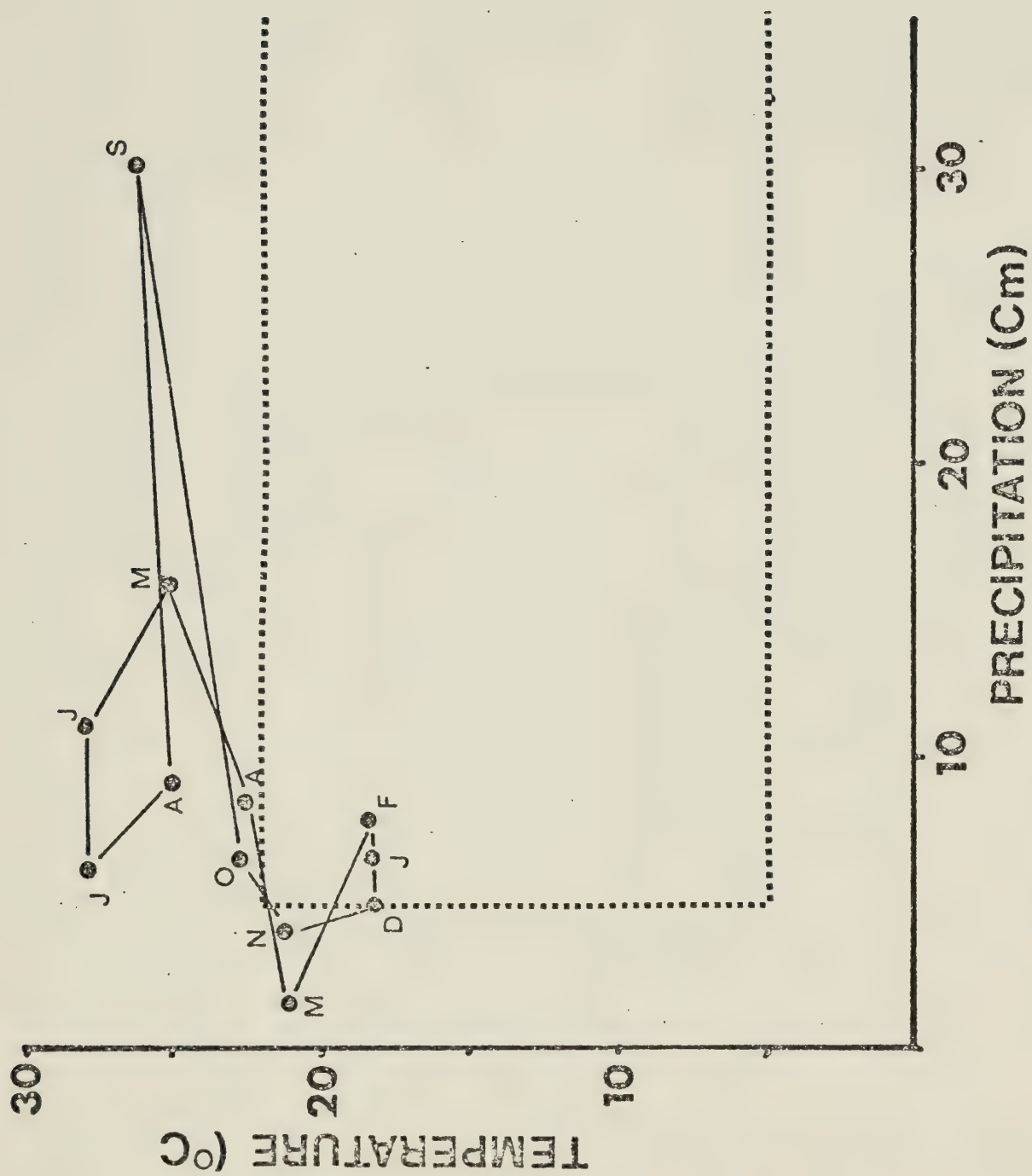
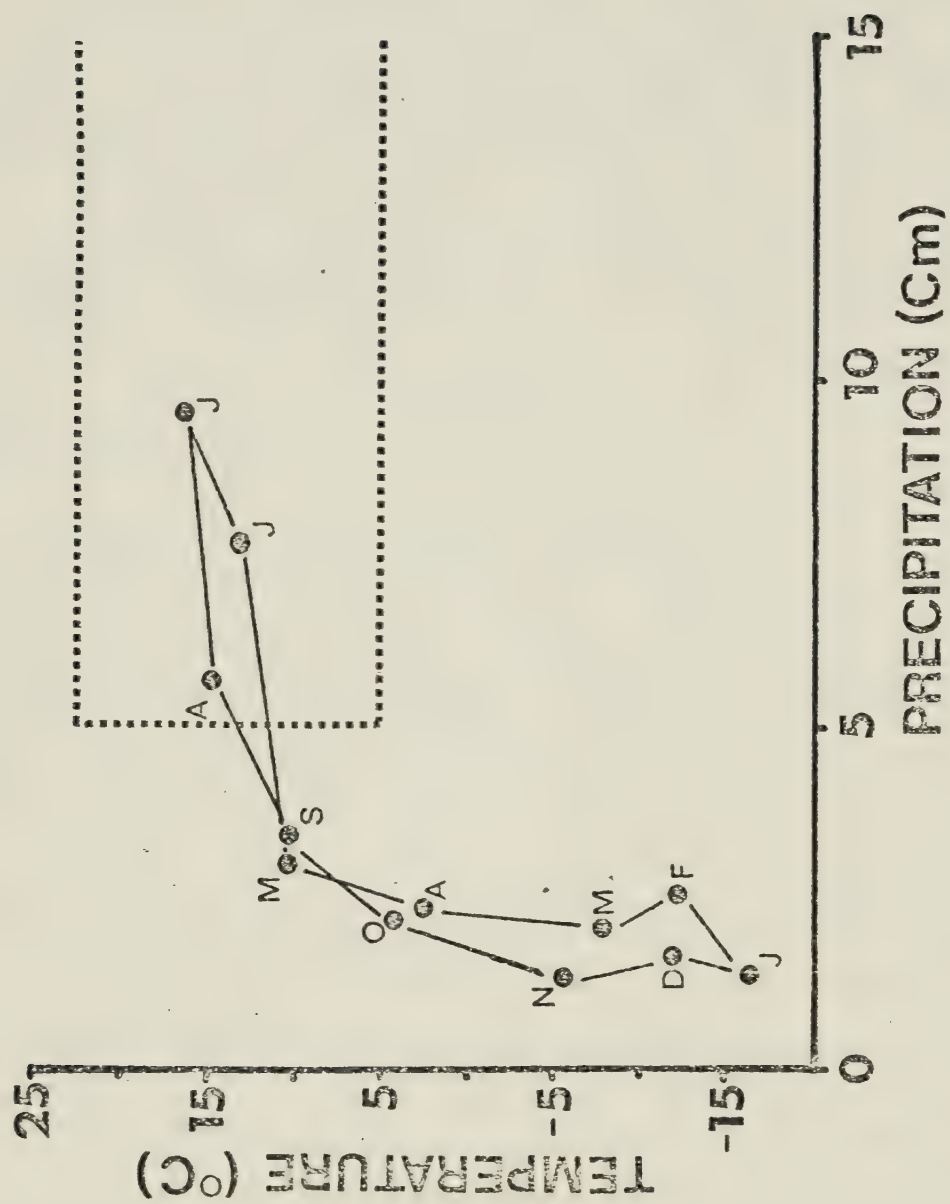


Figure 11. Bioclimatograph of Edmonton International Airport.
Dotted line delimits the region of maximum
transmission of *Ostertagia* species (Levine, 1963).
Ordinate is the mean monthly temperature, abscissa
is mean monthly precipitation.



Host sex was correlated with the mean number of *Nematodirella longissimespiculata*; females being more heavily infected than males. Prestwood *et al.* (1971) found differential infections of *Dictyocaulus viviparus* which they attributed to hormonal differences in white-tailed deer. During the breeding season, female rabbits (*Oryctolagus cuniculus*) have higher numbers of *Trichostrongylus retortaeformis* and *Graphidium strigosum* (Dunsmore, 1966a, 1966b). Thus, trichostrongylid nematodes may be particularly sensitive to hormonal changes. This may explain the observed correlation of *N. longissimespiculata* infections with host sex.

DISTRIBUTION OF THE PARASITE SPECIES IN ALBERTA

Among previous deer parasite studies, Beaudoin *et al.* (1969), Samuel (1969), Owen (1969), Prestwood *et al.* (1973) and Pursglove *et al.* (1976) considered geographic distribution of the parasites that they encountered. Often however, features of the external environment were considered to be less important than the association of host density, both intermediate and definitive, with the habitat type.

Over small, "climatologically homogeneous" sites, occurrence of certain parasite species may be correlated with a fine-grained view of the environment. For instance, Samuel (1969) attempted correlations of parasite prevalences and intensities with soil types and vegetation within the Welder Wildlife Refuge in Texas. Over larger geographic areas, such detailed analysis would prove physically impossible and even if accomplished, the resultant data set might prove too detailed to make any reasonable generalizations. Therefore, in order to derive any meaningful information, the scale of the surveyed area

must be matched with the coarseness of accompanying correlates.

Factors that might explain the variation in the parasite prevalences and intensities within Alberta include: deer densities, relative numbers of each species, density of other potential hosts, bioclimatic parameters and intermediate host distribution.

Dictyocaulus viviparus and *Trichuris* sp. were found mainly in mule deer from the prairies. Neither of these worms can be considered as being primarily mule deer parasites (although *Trichuris* could not be identified to species) but rather as parasites of domestic ruminants. Therefore, this distribution may be the result of a spillover of parasites from domestic to wild ruminants on the prairies where cattle and sheep husbandry is significant. Both of these worms have direct life-cycles so that the more moderate climatic conditions of southern Alberta may be favourable for survival of free-living infective stages. However, since *D. viviparus* is highly susceptible to desiccation (Rose, 1956), this explanation seems unlikely.

Members of the genus *Nematodirus* are highly resistant to desiccation and wide fluctuations in temperature (Poole, 1956; Marquardt *et al.*, 1959). The success of *N. helvetianus* and *N. odocoilei* in mule deer from Alberta is therefore not surprising. The large numbers of worms from the montane biome (Fig. 11) may be due to the greater mule deer densities and/or higher numbers of potential host wildlife species available (Soper, 1964).

In conjunction with the habitat zone correlations of parasites found in white-tailed and mule deer, there were conspicuous absences of several species of helminths. *Echinococcus granulosus* cysts have

been reported from both white-tailed and mule deer (Walker and Becklund, 1970). Cowan (1948, 1951) reported a single infected mule deer from Jasper, Alberta. Although deer make a significant contribution to the diet of wolves in Alberta (Mech, 1970 modified from Cowan, 1947), no cysts were found in the 60 deer examined in this study. Samuel *et al.* (1976) found 44% of moose over 16 months of age infected. Therefore, moose appear to be the major ungulate host involved in the sylvatic cycle in Alberta. Chances of encountering an infected deer were reduced since few samples originated from areas where wolf-deer interactions are common.

Fascioloides magna is regarded as a common parasite of wild ungulates including deer from many areas of North America. Swales (1935) investigated and elucidated aspects of the life-cycle of *F. magna* from Wainwright, Alberta where the parasite was considered enzootic. Results of the present study indicate the parasite is no longer present in deer of this region although suitable intermediate hosts are still present in the Wainwright area.

Histopathological and life-cycle considerations led Swales to conclude that cervids as opposed to bovids, were the primary definitive hosts. Lankester (1974) concluded that among cervids, moose were not the primary definitive host of liver flukes. Possibly wapiti (*Cervus elaphus*) or caribou (*Rangifer tarandus*) are the dominant hosts. Caribou seem unlikely candidates since historically, distributional overlaps with other hosts have been slight. An outbreak of fascioloidiasis in deer (species unspecified) in Italy was traced to an introduction of wapiti (Swales, 1935). Failure to find liver flukes in deer from

Alberta may be the result of a decreased number of interactions with wapiti where suitable intermediate hosts are present. One possible suitable site is southwestern Alberta, in the Bow River valley where heavily infected immigrating wapiti were examined by Flook and Stenton (1969). Unfortunately, few samples of deer were acquired from this area in the present study.

Differences in the distribution of gastro-intestinal parasites from mule deer and white-tailed deer from throughout the biomes of Alberta (Fig. 9) can be expressed by calculating similarity indices and plotting the results in a trellis diagram (Fig. 12). The similarity index used was the sum of percentages of the species common to a pair of samples (Holmes and Podesta, 1968).

Although this analysis can in some cases be misleading, it is instructive in the general case. The fauna from mule deer from the aspen parklands is most similar to the fauna from mule deer from the other zones. Since parkland is a transition habitat which borders all other habitat types except montane, this is an expected result. Using similar logic, mule deer from the montane zone should be the most dissimilar among mule deer; this was born out in the analysis. The situation is less clear for white-tailed deer since fewer were infected but, again, the average index value was higher for whitetails from the parklands than for the other zones. The zero value for montane vs. boreal white-tailed deer is artificially low but all montane white-tailed samples were from the southern part of the province, far from the boreal zone. In addition, the average similarity index value is lower when white-tailed deer are compared with mule deer than when either species is compared with itself.

Figure 12. Trellis diagram of similarity indices for helminths in white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) from the biomes of Alberta.

On a North American scale, the helminth faunas from deer of Alberta are in some respects unique. *Ostertagia odocoilei* is a commonly encountered white-tailed deer parasite in eastern North America whereas the presence of *O. ostertagi* in deer was considered "unusual" by Prestwood *et al.* (1973). *O. odocoilei* was absent in deer in Alberta and *O. ostertagi* seems to have replaced it: similar findings were recorded by Russell (1967) in white-tailed deer from southeastern British Columbia.

The other *Ostertagia* recovered from deer in Alberta was *O. bisonis*. *O. bisonis* has been found in mule deer from throughout western North America, mainly from the plains and prairies regions (Walker and Backlund, 1970). This species was originally described from specimens collected from bison of Wainwright, Alberta (Chapin, 1925). This is the first report of *O. bisonis* from white-tailed deer. Two deer were lightly infected, both from southern Alberta.

Setaria yehi, the only member of the genus found, occurred in 7% of the mule deer and 8% of the white-tailed deer examined. Becklund and Walker (1969) considered host specificity of *Setaria* spp. weak in ungulates and Samuel *et al.* (1976) found *S. labiatopapillosa* and *S. yehi* in moose that they examined from various regions of Alberta. However, *S. labiatopapillosa* was only found in moose of Elk Island National Park, an area where many bison are infected (Samuel, pers. comm.). The vectors of *S. yehi* and *S. labiatopapillosa* are not known in Alberta, but these data suggest that the differential feeding preferences of biting flies may be responsible for the separation.

Orthostrongylus macrotis (= *Protostrongylus macrotis*), is another worm found in both species of deer in Alberta which previously had only been reported from *O. hemionus* (Walker and Becklund, 1970) and *Antilocapra americana* (Greiner *et al.*, 1974) and *Alces alces* (Samuel *et al.*, 1976). The cattle lungworm, *Dictyocaulus viviparus* was more abundant in both species (Fig. 5). A mixed *Orthostrongylus*, *Dictyocaulus* infection was detected in one white-tailed deer. *Dictyocaulus* infections are commonly encountered in deer wherever cattle husbandry is important. *Orthostrongylus* infections are restricted to western North America, closely associated with the range of mule deer.

Nematodirus odocoilei and *N. helvetianus* were abundant parasites of mule deer but were absent in white-tailed deer. *N. odocoilei* is a common parasite of both deer species throughout the rest of North America (Walker and Becklund, 1970). *N. spathiger* and *N. abnormalis* have also been reported from mule deer. *N. helvetianus* is normally associated with domestic sheep but Russell (1967) found both whitetails (1 out of 52) and mule deer (6 out of 6) infected.

Nematodirella longissimespiculata, like *Nematodirus* spp. was found only in mule deer. Cowan (1946, 1951) provided the only other North American reports of *N. longissimespiculata* infections in deer. *O. hemionus* collected from coastal British Columbia were infected.

Skrjabinema parva, the pinworm, has been previously found in mule deer from California (Schad, 1959), Colorado (Olsen and Tolman, 1950), Idaho (Dikmans, 1942) and Montana (Worley and Eustace, 1972). Samuel and Trainer (1969) and Russell (1967) found *S. parva* in white-tailed deer in Wisconsin and British Columbia, respectively.

Both whitetails and mule deer were infected in Alberta with higher prevalence and intensity infections in mule deer (Table I).

COMMUNITY ANALYSIS

Robert MacArthur characterized science as a "... search for repeated patterns" (MacArthur, 1972). In order to evaluate patterns at a community level, one cannot simply investigate the population dynamics of each contributing species in the community. Community ecologists have, therefore, derived measurable attributes so that communities could be compared. If we consider the gastro-intestinal helminths of mule deer and white-tailed deer as communities, we can attempt to evaluate their characteristics, compare the communities and thus, search for patterns.

Examination of the parasite profiles of white-tailed, black-tailed and mule deer (Fig. 5) shows that although several helminths are found in all three species of deer, the relative abundance of each species differs considerably. *Dictyocaulus viviparus*, which is the most abundant species in the white-tailed deer, makes only a minor contribution in the mule deer community. The situation is reversed for *Skrjabinema parva*, which is replaced in black-tailed deer by *Oesophagostomum venulosum*. *Nematodirus* spp. and *Nematodirella longissimespiculata* are abundant in mule deer only.

Overall patterns can be characterized to a certain extent by a single value, the diversity index. One "index" often used to describe communities is simple species richness. Mule deer harbored a richer community than either white-tailed deer (16 vs 11) or black-tailed

deer (16 vs 11), however, the small sample size of black-tailed deer examined (13) probably resulted in an under-estimate of the total fauna of that host. Cowan (1946, 1951) examined over 100 Columbian black-tailed deer and found 13 species of gastro-intestinal parasites.

Species richness values fail to consider the equitability or evenness of distribution of the organisms in a community. Therefore, indices have been developed which increase both as species richness increases and as species are found more evenly distributed. None of the indices are suitable for all purposes. In certain cases they may yield results that are not mutually consistent (Hurlbert, 1971). Simpson's index of diversity gives relatively little weight to rare species whereas the Shannon-Weaver function allots them more importance (Pielou, 1975). Squires and Wistendahl (1977) showed that areal species richness, when compared to either the Shannon-Weaver and Simpson's indices, was more uniformly affected by both species richness and the equitability components. Therefore, in order to estimate the diversity in white-tailed and mule deer gastro-intestinal helminth communities, all three indices were calculated (Table VIII). In addition, the Shannon-Weaver function was calculated using only prevalence rather than abundance.

These indices tend to show that in Alberta, mule deer are host to richer, more diverse helminth faunas although the Shannon-Weaver function, based on abundance, was slightly higher for white-tailed deer. This resulted from the contribution to the index made by the equitability factor which more than compensated for the lower species

richness found in white-tailed deer. Areal species richness confirmed that the community in mule deer was more diverse ($t_s = 5.67$, $P < 0.001$) than that in white-tailed deer. Surprisingly, although areal species richness was higher in black-tailed deer than in mule deer ($t_s = 3.12$, $P < 0.01$), this was not reflected in any of the other indices. This probably resulted from the dominance in the black-tailed helminth community demonstrated by *Nematodirus odocoilei* which is indicated by the low equitability value.

Patterns in species richness and diversity of free-living organisms on a continental basis have been noted for many years. Dogiel *et al.* (1964) proposed some general rules to explain the composition of a host's parasite fauna over large geographic regions. One correlation that Dogiel considered was the abundance and mode of life of a host with the abundance and composition of its parasites. Dogiel conjectured that when two similar host species who have the ability to harbour the same parasites and overlap in distribution, the rarer host will have a smaller parasite fauna. Furthermore, if host density decreases towards the edge of its range, then host animals at the edge of the range should have lower intensity infections than those animals which are centrally located.

White-tailed and mule deer would seem to fulfill the host criteria established by Dogiel. Today, white-tailed deer and mule deer are sympatric over much of western North America including Alberta (Fig. 1). Whitetails were first reported in the North Saskatchewan River valley as early as 1787 (Webb, unpublished). In the 1870's, deer of both species were frequently noted along river

valleys in the south central part of the province although it is believed that numbers had not increased substantially during this time. At the turn of the century, major die-offs of all Alberta ungulates occurred which have been attributed to increased human utilization and severe winter weather. Since that time, both deer species increased in numbers substantially and expanded their ranges north and westward; first mule deer and later whitetails. Today, the white-tailed deer is the dominant species in the prairies and eastern aspen parklands while mule deer still predominate in the mountains (Soper, 1964; Kramer, 1972).

Based on Dogiel's hypothesis therefore, white-tailed deer in Alberta, at the northern edge of their range, should have fewer species of parasites and lower intensity infections than deer from the center of their range, the south-central United States. In addition, white-tailed deer in Alberta, in the aspen parklands and prairies (where they are most abundant) should have greater infections than elsewhere in the province. Similarly, mule deer in Alberta should have lighter intensity, less species rich infections than mule deer in the west-central United States.

Diversity of faunas can be compared by computing diversity indices from data presented in surveys from throughout North America. The Shannon-Weaver index was used because of its ease of calculation and because it is widely used in the literature when comparisons are made on a continental scale (e.g. Humphrey, 1975). Unfortunately, most parasite studies fail to provide the absolute and total number of worms found, therefore, prevalence data had to be incorporated as a poor substitute for abundance in the calculations. Pielou's

equitability measure, J, was also calculated for each survey. In addition, Simpson's index was calculated using percent prevalence as the "importance value" (Holmes and Podesta, 1968). To maintain continuity with the other indices, the difference of one minus Holmes and Podesta's "C" was plotted (Fig.s 13 and 14). Simple species richness was appraised, but included only those parasites that could be detected using the necropsy techniques employed in this survey. When helminths were not identified to species, only one species was assumed to be present. Because simple species richness is sensitive to sample size, Margalef's (1964), Odum *et al.*'s (1960) and Henhinick's (1964) species richness indices, which incorporate sample size, were calculated (Table XII). Since they confirmed the results obtained from analysing simple species richness, however, they will largely be excluded from the remainder of the discussion.

When the white-tailed deer parasite fauna was examined in this way, Dogiel's hypothesis was confirmed. The deer near the center of their range, Arkansas and the southeastern United States had much higher intensity infections (Owen, 1969; Prestwood *et al.*, 1973) and almost double the number of species (23 and 20 vs. 14 and 11) than deer near the edge of their range in British Columbia and Alberta. Often, however, diversity index values were very similar between sites and should be interpreted with caution, particularly since, by necessity, calculations were based on prevalence. The impoverished fauna from white-tailed deer in Massachusetts (St. Armand, 1977), may demonstrate a peninsular effect (MacArthur and Wilson, 1967), since species richness is low even when sample size ($N = 33$) was considered (Table XII).

Calculations of similarity indices (Fig. 15) showed that white-tailed

Figure 13. Simpson's index of diversity for gastro-intestinal helminths of white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) in North America. Data for white-tailed deer derived from Russel (1968), Boddicker and Huggins (1969), Cook (1972), St. Armand (1976), Prestwood (1971), Prestwood *et al.* (1971), Samuel (1969) and Owen (1969). Data for mule deer derived from Boddicker and Huggins (1969) and Worley and Eustace (1969).



Figure 14. The Shannon-Weaver (H' prev.) index of diversity (top number), species richness (S) (middle number) and equitability (J) (bottom number) values for gastrointestinal helminths of white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) in North America. Data sources as in preceeding figure.

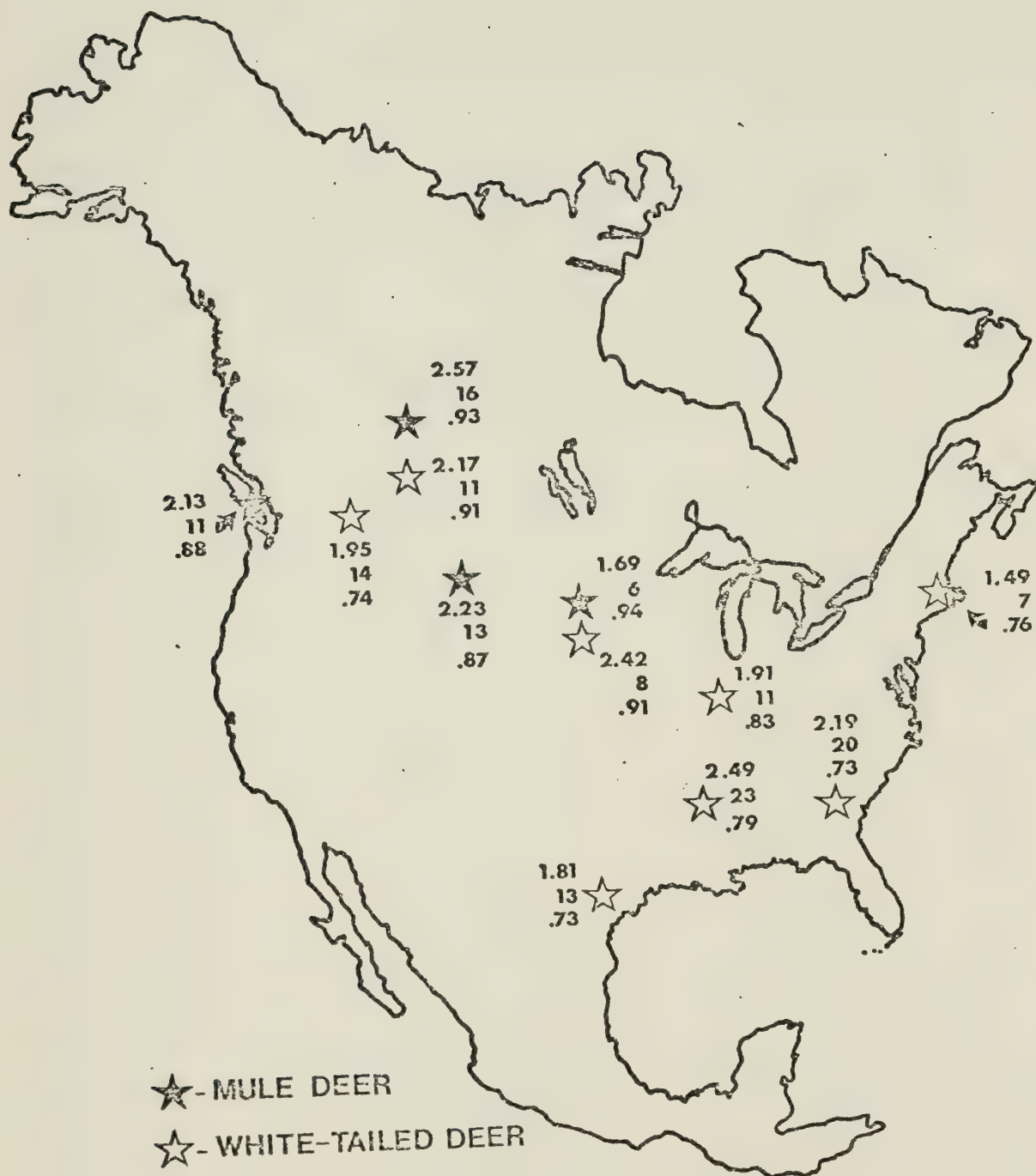


TABLE XII. Species richness measures of deer helminth communities from throughout North America.

	S	N	R ₁	R ₂	R ₃
WHITE-TAILED DEER					
Alberta (this study)	11	60	5.62	6.19	1.42
British Columbia (Russell, 1968)	14	69	7.07	7.61	1.69
South Dakota (Boddicker and Huggins, 1969)	8	83	3.65	4.17	0.88
Illinois (Cook, 1972)	10	40	5.66	6.24	1.58
Massachusetts (St. Armand, 1976)	7	33	3.95	4.61	1.22
S.E. United States (Prestwood, 1971)	22	806	7.22	7.57	0.77
Texas (Samuel, 1969)	13	146	5.54	6.01	1.08
Arkansas (Owen, 1969)	23	143	10.21	10.67	1.92
MULE DEER					
Alberta (this study)	16	60	8.44	9.00	2.07
British Columbia (this study)	11	13	8.98	9.87	3.05
British Columbia (Cowan, 1946, 1951)	13	138	5.62	6.08	1.11
Montana (Worley and Eustace, 1969)	13	44	7.30	7.91	1.96
South Dakota (Boddicker and Huggins, 1969)	6	30	3.38	4.06	1.10

S = number of species, N = sample size, $R_1 = \frac{(S-1)}{\log N}$ (Margalef, 1951), $R_2 = \frac{S}{\log N}$ (Odum *et al.* 1960), $R_3 = \frac{S}{N^{1/2}}$ (Menhinick, 1964).

deer from Alberta were most similar to whitetails from southeastern British Columbia. This is expected since the British Columbia study was conducted near the Alberta border in southeastern B.C. (Fig. 15). This may reflect a mixing or migration of deer through the mountain passes in southern Alberta. Another center of similarity was the southeastern United States. Deer in Arkansas shared 10 species of parasites with deer from Texas and 9 with those from the southeastern United States (Fig. 15). Although similarity was inversely correlated with distance between survey sites, this merely indicates differences in biomes. For instance, most deer sampled from the southeastern United States were from the coastal plains. Deviating from this pattern however, is Samuel's (1969) Texas study. Perhaps the extreme climatic conditions experienced in this area are partially responsible for the unexpectedly low species richness values.

The situation for mule deer parasites was less clear, partially because of the lack of data for deer from all of its southern range. Mule deer from Montana (near the center of the mule deer range) had twice as many species of gastro-intestinal parasites, more diverse and more intense infections than deer from near the edge of their range in South Dakota (Fig. 16), as one would expect from Dogiel's hypothesis. The black-tailed deer from Vancouver Island had a less diverse fauna than mule deer from Montana but intensities of infection were greater in British Columbia. This may result from the isolated island position of the blacktails.

The mule deer of Alberta, nearer the edge of the range than those in Montana, appeared to have a richer, more diverse parasite

Figure 15. Trellis diagram of similarity indices of white-tailed deer (*Odocoileus virginianus*) gastro-intestinal helminths, and number of common species among survey sites. (Data from sources cited in Figure 13).

Figure 16. Trellis diagram of similarity indices of mule deer (*Odocoileus hemionus*) gastro-intestinal helminths, and number of species in common among survey sites. (Data from sources cited in Figure 13).



fauna. Moreover, intensities of infection as well as prevalences were almost identical between the two regions as is reflected in the high similarity index value (Fig. 16).

Although absolute host density data for either Alberta or Montana are lacking, mule deer in Alberta appear to be less abundant than mule deer in Montana (W.M. Samuel, J.C. Holmes, pers. comm.) and their helminth fauna should, therefore, follow Dogiel's rule.

The Montana samples were collected from "semiarid rangeland", thus a comparison with mule deer from all of the biomes of Alberta is, perhaps, unjustified. When compared only with deer from the prairies of Alberta ($N = 16$), Dogiel's hypothesis was confirmed. Mule deer from the prairies were infected with 10 species of parasites and had an H' (prevalence) value of 2.13 as opposed to 2.23 and 10 species in Montana. Simpson's index values were virtually identical between the two sites. Equitability was, nevertheless, higher in Alberta (0.93 vs 0.87).

Equitability of parasites in both deer species is particularly high in Alberta (Fig. 14). Similar high equitability results were obtained in South Dakota, the only other study which looked at both species. In all cases, the magnitude of J values is artificially high due to the use of prevalence as an estimate of abundance, hence, direct comparisons with J values from free-living animal or plant community studies would be misleading.

Within Alberta itself, we would expect mule deer in areas where they are most abundant, the mountains, foothills and deeper-snow areas of the prairies (Webb, unpublished), to have richer, more diverse helminth infections than those from other

biomes. Conversely, white-tailed deer should have richer and heavier infections in the parklands, grasslands, boreal-parkland transition and lower latitude regions of Alberta, where the populations are densest (Webb, unpublished); if Dogiel's hypothesis holds true.

White-tailed deer confirmed Dogiel's hypothesis. The diversity indices consistently identified the prairies and aspen parkland as being associated with the most diverse white-tailed helminth communities (Figs. 17 and 18) (Table XIII). Simple species richness (as well as species richness measures which control for sample size (Table XIV)) showed the same trend. Areal species richness, however, did not vary significantly in any of the biomes.

In mule deer, the indices indicated incongruities. Simpson's index values are all very close but the aspen parklands ranked as the biome with the highest value (Table XV). Because of small sample sizes, the mountains and foothills were analysed as a group as well as individually. The Shannon-Weaver function tended to agree more closely than 1-C with Dogiel's hypothesis. The prairies and foothills provided the highest values (Fig. 19) (Table XV). The disparity between the two indices can be partially explained by examination of equitability. The J value of the aspen parklands was low, thus, the high diversity value indicated by Simpson's index probably resulted from a large contribution to the index by species richness.

Species richness values (Tables XIV, XV) (Fig. 18) tended to confirm Dogiel's hypothesis. Mule deer in the montane biome had significantly more species of parasites per deer than mule deer from

Figure 17. Shannon-Weaver index (H'), equitability (J) and species richness (S) of gastro-intestinal helminths of white-tailed deer (*Odocoileus virginianus*) from the habitat zones of Alberta with relative density of deer.

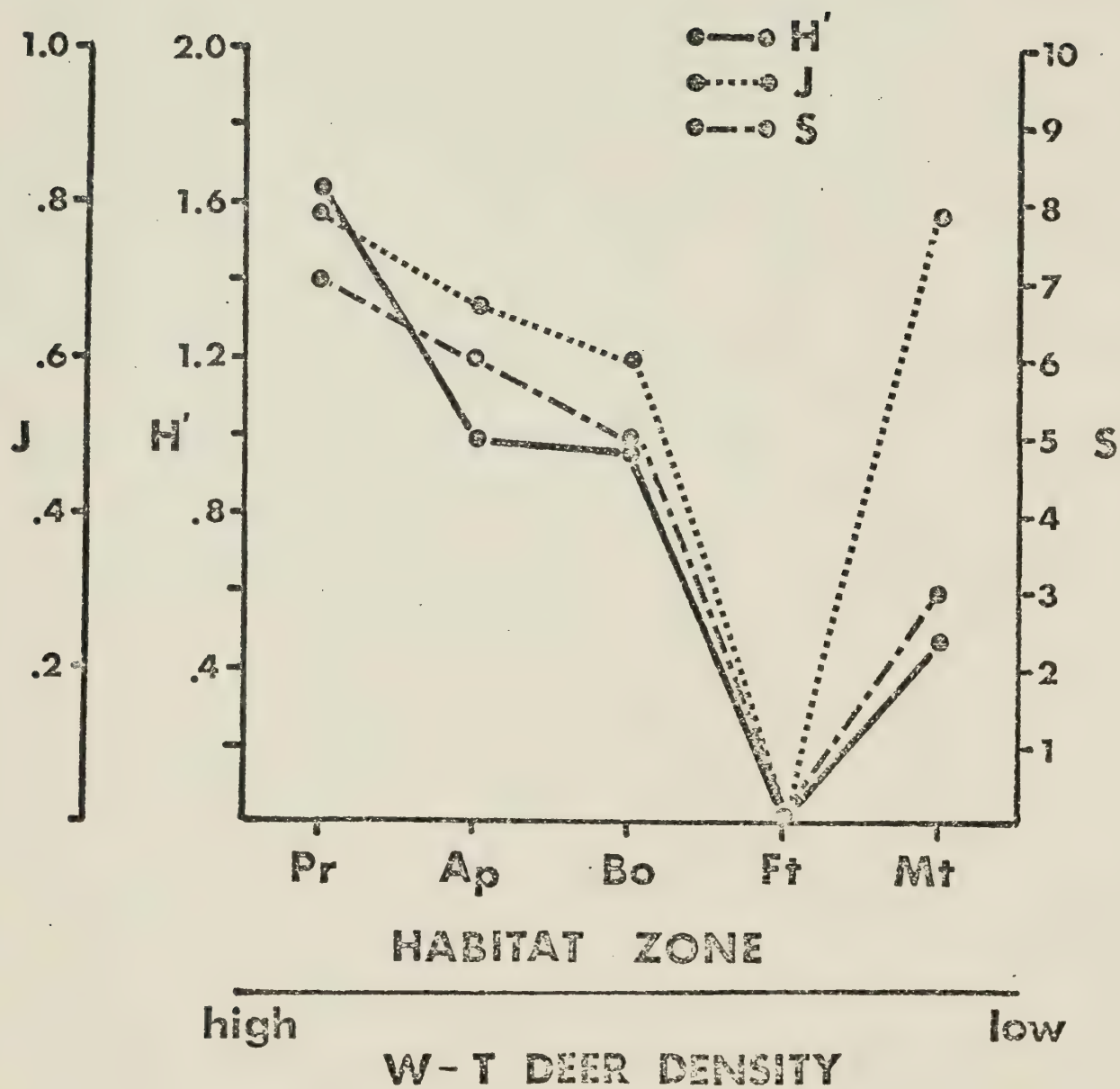


Figure 18. Areal species richness (± 1 S.E.) of gastrointestinal helminths of white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*) from the habitat zones of Alberta. (N = sample size).

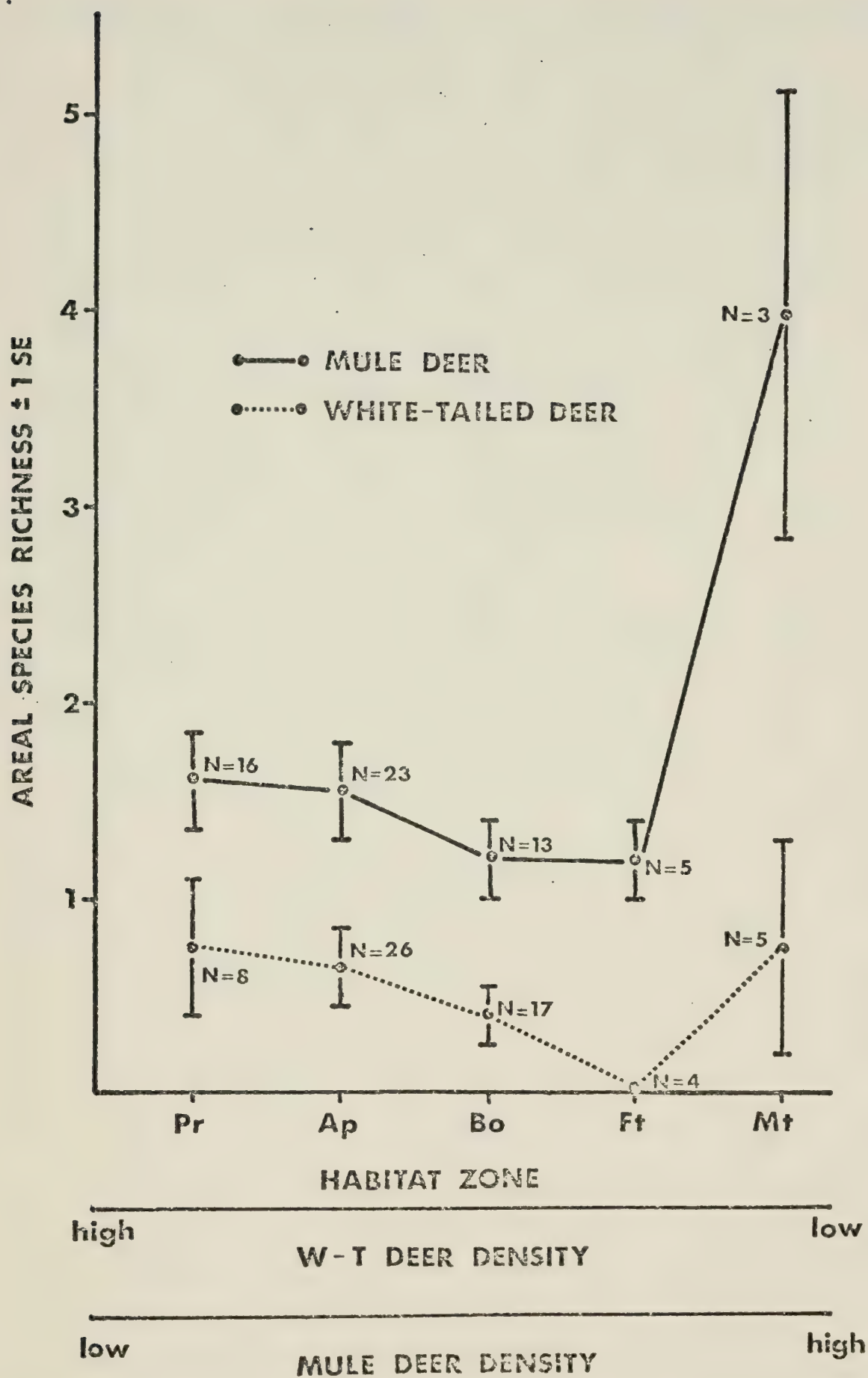


TABLE XIII. Simpson's index (1-C), Shannon-Weaver index (H'), equitability (J), species richness (S) and sample size (N) of white-tailed deer (*Odocoileus virginianus*) gastro-intestinal helminths from the habitat zones of Alberta.

	1-C	H'	J	S	N
Prairies	.86	1.63	.79	7	8
Aspen Parkland	.80	1.19	.67	6	26
Boreal Forest	.75	.97	.60	5	17
Foothills	-	-	-	0	4
Montane	.56	.50	.79	3	5

TABLE XIV. Species richness measures of deer helminth communities
from five biomes in Alberta.

	S	N	R ₁	R ₂	R ₃
WHITE-TAILED DEER					
Aspen Parklands	6	26	3.53	4.24	1.18
Boreal Forest	5	17	3.25	4.06	1.21
Prairies	7	8	6.64	7.75	2.47
Foothills	0	4	-	-	-
Montane	3	5	2.86	4.29	1.34
MULE DEER					
Aspen Parklands	13	23	8.81	9.19	2.71
Boreal Forest	10	13	8.08	8.98	2.77
Prairies	14	16	10.80	11.63	3.50
Foothills	5	5	5.72	7.15	2.24
Montane	7	3	12.58	14.67	4.04

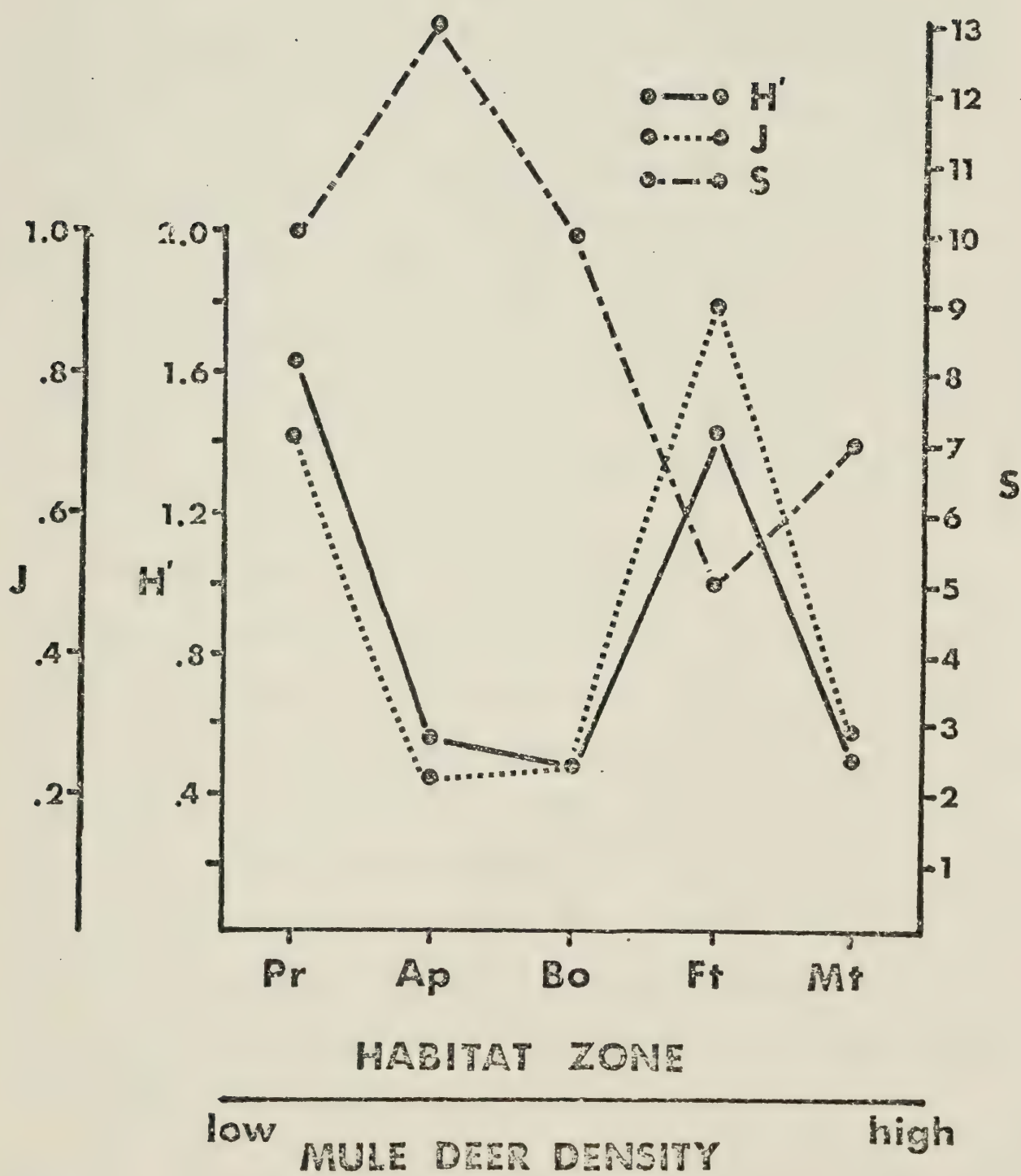
S = number of species, N = sample size, $R_1 = \frac{(S-1)}{\log N}$ (Margalef, 1951)

$R_2 = \frac{S}{\log N}$ (Odum *et al.*, 1960) and $R_3 = \frac{S}{N^{1/2}}$ (Menhinick, 1964).

TABLE XV. Simpson's index (1-C), Shannon-Weaver index (H'), equitability (J), species richness (S) and host sample size (N) of mule deer (*Odocoileus hemionus*) gastro-intestinal helminths from the habitat zones of Alberta.

	1-C	H'	J	S	N
Prairies	.86	1.63	.71	10	16
Aspen Parklands	.89	.58	.23	13	23
Boreal Forest	.88	.50	.22	10	13
Foothills	.78	1.46	.90	5	5
Montane	.83	.55	.29	7	3
Foothills + Montane	.89	.72	.30	11	8

Figure 19. Shannon-Weaver (H') index, equitability (J) and species richness (S) of gastro-intestinal helminths of mule deer (*Odocoileus hemionus*) from the habitat zones of Alberta with relative density of deer.



the prairies ($t_s = 3.19$, $P < 0.01$) (Fig. 18).

According to Dogiel's hypothesis, white-tailed deer should have richer, more diverse infections in the parklands and prairies than mule deer whereas mule deer infections should be predominant in the foothills and montane biome. In the prairies, white-tailed and mule deer had virtually identical H' values (Figs. 17, 19) (Tables XIII, XV). Areal species richness showed mule deer to have a slightly richer fauna in the prairies but the difference was not significant ($t_s = 1.71$, $P > 0.05$) (Fig. 18). In the parkland, mule deer had a significantly higher areal species richness than whitetails ($t_s = 3.65$, $P < 0.01$) (Fig. 18) and were infected with 81% of the total possible number of gastro-intestinal parasite species found in mule deer in Alberta as opposed to 55% for white-tailed deer (Figs. 17, 19). It appears, therefore, that mule deer had a richer fauna in the prairies and parkland than is predicted by Dogiel's rule.

Several explanations for this incongruity in the areal species richness and diversity findings are possible. Perhaps mule deer are indeed more abundant in the aspen parklands and prairies of Alberta than Soper (1964), Webb (unpublished), Kramer (1972) and others have suspected. Perhaps bioclimatic or other intrinsic properties of the parklands promoted a richer parasite pool to draw upon which eclipsed host density considerations. Menge and Sutherland (1976) listed time, spatial heterogeneity, competition, predation, climatic stability, productivity and combinations of these factors as affecting species diversity in free-living systems. None of these factors seems

suitably different between whitetails and mule deer to account for the difference.

One intriguing possibility is based on an hypothesis proposed by Barbehenn (1969). He suggested that the outcome of competition between two host species may be mediated by parasitism. If two competing host species can share the same parasites, then one of those species may be differentially sensitive to the effects of parasitism such that the competitive interaction between them will be influenced. Therefore, Barbehenn suggested that certain parasites may be maintained in one host species as a weapon of competition. Corollaries of Barbehenn's hypothesis are that: 1) hosts which are utilizing parasites will be restricted to refuges against invaders and 2) that host-parasite co-adaptation is maximal where host species diversity (i.e. competition) is minimal. One would expect therefore, that such a host would attempt to strike a balance between pathogenic effects and parasite species diversity.

Evidence from Bush's (1973) analysis of dominance does not support Barbehenn's hypothesis. Parasites can be assigned to certain dominance classes which describe, to some extent, host-parasite specificity in the system. In white-tailed deer, 10 out of the 11 (91%) of the species were classified as dominants, and 10 out of 11 (9%) was co-dominant (Table IX). In mule deer, 9 out of 16 (56%) of the parasites were dominants and 7 (44%) were co-dominants. Therefore, mule deer have a higher proportion of species which, although characteristic of the community, do quite well in other hosts. If a host is controlling the diversity of its helminth fauna, then it must be well adapted to

control its parasites. Therefore, one might expect a higher proportion of dominants in such a host. This refutes one of the corollaries put forward by Barbehenn; where host competition is extreme, host-parasite co-adaptation must be greatest. Unfortunately, dominance analysis breaks down in certain instances. Although *D. viviparus* is classified as a dominant, geographic distribution and other considerations suggest that cattle are the true dominant host. Probably, parasite data for all potential host species in a system are necessary to make conclusive use of dominance analysis. The correlates of the dominance classes proposed by Bush (1973), are probably not directly applicable to ungulate parasites. Redefining the dominance classes used might make the analysis more suitable. In addition, Bush's analysis was applied to a trematode dominated system in which definitive host specificity via maturation control was important. Ungulate nematode host specificity seems to be rather loose and not mediated through definitive host maturation processes. The low intensity infections found also created some misleading results. For instance, *Ostertagia bisonis* infections in white-tailed deer were scattered and infrequent yet this parasite is classified as dominant. Redefinition of dominance classes would eliminate these problems.

Support for Dogiel's hypothesis has come from studies of the parasite fauna of *Rutilus rutilus* in Europe by Rumyantsev (1975). Halvorsen (1971) however, found that Dogiel's hypothesis did not hold true when he examined the parasite fauna of coarse fish (roach, burbot, bream, etc.) from southeastern Norway. Perhaps the discrepancy results from competitive interactions between or among two or more of these fish species.

Although difficult to prove or disprove directly, parasitologists studying helminth faunas of ecologically closely related species should be aware of ecological interactions between hosts and the possible effects on parasite faunas.

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APPENDIX I. Age, sex, season and habitat zone of capture of
white-tailed deer examined for gastro-intestinal
helminths.

Necropsy #	Habitat Zone	Age (mo)	Sex	Season	Necropsy #	Habitat Zone	Age (mo)	Sex	Season
3	Pr	66	♀	A	69	Mt	8	♂	W
14	Bo	6	♀	A	70	Ap	43	+	W
15	Ap	21	♂	W	71	Ap	6	+	A
17	Pr	--	♂	A	72	Bo	--	+	Su
18	Fo	39	♀	W	73	Ap	--	-	A
19	Ap	--	+	A	74	Ap	--	-	A
20	Mt	18	♂	A	75	Ap	8	+	W
22	Bo	18	♂	A	76	Ap	6	♂	A
23	Bo	12	♂	Su	77	Ap	6	+	Su
26	Bo	12	♂	Su	78	Ap	9	+	W
28	Bo	40	-	W	80	Pr	10	+	Sp
29	Ap	7	♀	W	*83	Ap	24	+	A
32	Bo	7	♂	W	84	Ap	6	+	A
33	Pr	24	♀	Sp	85	Ap	6	♂	A
34	Fo	6	+	A	86	Ap	78	+	A
35	Ap	6	♂	A	87	Bo	43	+	W
37	Ap	42	♀	A	88	Bo	13	♂	Su
38	Bo	54	+	A	89	Ap	--	♂	W
39	Bo	42	♂	A	90	Ap	12	♂	A
40	Mt	6	♂	A	91	Ap	83	+	Sp
41	Pr	--	♀	W	92	Ap	6	♂	A
42	Ap	--	♂	W	93	Ap	6	+	A
43	Bo	11	♂	Sp	95	Ap	--	+	W
44	Bo	11	♀	Sp	113	Bo	--	♂	A
45	Ap	6	+	A	116	Pr	--	♂	W
46	Bo	7	♂	W	117	Pr	--	+	W
49	Ap	12	♂	A	119	Mt	--	+	W
62	Bo	18	♂	A	121	Fo	--	+	W
65	Ap	9	♀	W	122	Pr	--	+	W
67	Bo	23	♂	Sp	123	Fo	--	♂	W
68	Mt	33	♂	W					

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8	Pr	$\bar{x}=20.6$	30 ♀	26 A
17	Bo	12 Ad	27 ♂	23 W
26	Ap	22 Fa	3?	6 Sp
4	Fo	10 Yr		5 Su
5	Mt	± 2.9		
		(S.E.)		

J-J-A = Su Pr = Prairie
 S-O-N = A Bo = Boreal Forest
 D-J-F = W Ap = Aspen Parkland
 M-A-M = Sp Fo = Foothills
 Mt = Mountains

0 - 11 = fawn (Fa) Su = summer
 12 - 23 = yearling (Yr) A = autumn
 24 → = adult (Ad) W = winter
 Sp = spring

* not considered in analysis (incomplete necropsy)

APPENDIX II. Age, sex, season and habitat zone of capture of
mule deer examined for gastro-intestinal helminths.

Necropsy #	Habitat Zone	Age (mo)	Sex	Season	Necropsy #	Habitat Zone	Age (mo)	Sex	Season
1	Pr	--	♀	A	94	Bo	--	♂	W
2	Ap	--	♀	--	96	Pr	--	♂	W
4	Ap	6	♂	W	97	Ap	--	♂	W
5	Ap	9	♀	W	98	Ap	--	♂	W
6	Bo	10	♀	Sp	99	Bo	--	♂	W
7	Ap	34	♂	Sp	100	Pr	--	♂	W
8	Pr	21	♂	W	101	Pr	--	♂	W
9	Ap	9	♀	W	102	Bo	--	♂	W
10	Bo	10	♀	Sp	103	Pr	--	♂	W
11	Pr	20	♀	W	104	Bo	--	♂	W
12	Pr	20	♂	W	105	Pr	--	♂	W
13	Pr	8	♂	W	106	Ap	--	♂	W
19	Ap	--	♀	A	107	Pr	--	♀	W
21	Fo	10	♀	Sp	108	Ap	--	♀	W
24	Bo	--	♀	Sp	109	Bo	--	♂	A
25	Fo	39	♀	Su	110	Pr	--	♀	W
30	Ap	18	♀	A	111	Mt	--	♀	W
31	Bo	30	♂	A	112	Pr	--	♀	W
36	Pr	30	♂	A	114	Bo	--	♀	W
47	Ap	24	♂	A	115	Bo	--	♀	W
48	Fo	47	♀	Sp	118	Fo	--	♂	A
50	Bo	12	♀	Sp	120	Mt	--	♀	W
51	Ap	66	♀	A	124	Bo	--	♀	W
52	Ap	24	♂	A	125	Pr	--	♀	W
61	Ap	12	♂	A	126	Ap	--	♀	W
63	Ap	12	♂	A	127	Fo	--	♂	W
66	Ap	12	♂	A	128	Ap	--	♂	A
79	Ap	24	♂	A	129	Ap	--	♂	W
81	Mt	11	♂	Sp	130	Pr	--	♂	W
82	Ap	24	♂	A	131	Mt	--	♂	-

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16	Pr	$\bar{x}=20.0$	29	♀	16	A	
22	Ap	10	Ad	30	♂	33	W
13	Bo	8	Yr			8	Sp
5	Fo	7	Fa			1	Su
4	Mt						

J-J-A = Su Pr = Prairie
 S-O-N = A Bo = Boreal Forest
 D-J-F = W Ap = Aspen Parkland
 M-A-M = Sp Fo = Foothills
 Mt = Mountains

0 - 11 = fawn (Fa) Su = summer
 12 - 23 = yearling (Yr) A = autumn
 24 → = adult (Ad) W = winter
 Sp = spring

APPENDIX III. Age class, sex, season of capture and collection site of Columbian black-tailed deer examined for gastrointestinal helminths.

Necropsy #	Collection Site	Age	Sex	Season
53	Mid J Slash N.W. Bay	Adult	♀	Spr (March)
54	Okay Mt Timber N.W. Bay	Adult	♀	Spr (March)
55	Err Slash N.W. Bay	Fawn	♀	Spr (March)
56	L Road N.W. Bay	Fawn	♂	Spr (May)
57	Okay Mt Timber N.W. Bay	Fawn	♂	Spr (March)
58	Okay Clearcut N.W. Bay	Fawn	♀	Win (Jan)
59	Upper J Slash N.W. Bay	Adult	♀	Spr (May)
60	Err Slash N.W. Bay	Adult	♀	Spr (March)
132	N.W. Bay	-	♂	Spr (April)
133	K Road N.W. Bay	Fawn	♂	Spr (March)
134	Namaimo Lks.	Adult	♀	Spr (April)
135	N.W. Bay	-	♂	Spr (March)
136	N.W. Bay	Adult	♀	Spr (March)
TOTS.				
13		6 Adults 5 Fawns 2 ?	8 ♀♀ 5 ♂♂	12 Spring 1 Winter

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